

1 **Plant Physiology Increases the Magnitude**
2 **and Spread of the Transient Climate**
3 **Response in CMIP6 Earth System Models**

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15 **Abstract:**

16 Increasing concentrations of CO₂ in the atmosphere not only influence climate
17 through CO₂'s effect as a greenhouse gas but also through its impact on plants. Plants
18 respond to atmospheric CO₂ concentrations in several ways that can alter surface energy
19 and water fluxes and thus surface climate, including changes in stomatal conductance,
20 water use, and canopy leaf area. These plant physiological responses are already
21 embedded in Earth system models, and a robust literature demonstrates that they can
22 affect global-scale temperature. However, the physiological contribution to transient
23 warming has yet to be assessed systematically in Earth system models. Here this gap is
24 addressed using carbon cycle simulations from the 5th and 6th phases of the Coupled
25 Model Intercomparison Project (CMIP) to isolate the radiative and physiological
26 contributions to the transient climate response (TCR). In CMIP6 models, the
27 physiological effect contributes 0.11°C (standard deviation: 0.10°C; range: 0.02 - 0.29°C)
28 of warming to the TCR, corresponding to 5.2% of the full TCR (standard deviation:
29 4.1%; range: 1.4 - 13.9%). Moreover, variation in the physiological contribution to the
30 TCR across models contributes disproportionately more to the inter-model spread of
31 TCR estimates than it does to the mean. The largest contribution of plant physiology to
32 CO₂-forced warming – and the inter-model spread in warming – occurs over land,
33 especially in forested regions.

34

35 **1. Introduction**

36 Increasing concentrations of atmospheric CO₂ alter global temperature through
37 both CO₂'s role as a greenhouse gas within the atmosphere (radiative effect) and
38 through plants' response to CO₂ at the land surface (physiological effect). Plants
39 respond to atmospheric CO₂ concentrations by regulating their stomata (pores on the
40 leaves which modulate the exchange of CO₂ and water vapor between the leaf and the

41 atmosphere), changing water use, adjusting canopy leaf area, and ultimately, changing
42 species composition and vegetation cover. These plant physiological responses to higher
43 CO₂ can influence land surface temperature by altering land evapotranspiration, surface
44 albedo, and surface roughness, which are important controls over the fluxes of water and
45 energy between the land surface and the atmosphere. Here we use the term
46 “physiological effect” to encompass the net effect of all plant responses to increasing
47 CO₂, but note that in some past work the term refers solely to the effect of changes in
48 stomatal conductance (e.g. Skinner et al. 2018).

49 Plant responses to CO₂ modulate land evapotranspiration through two opposing
50 mechanisms. Higher concentrations of CO₂ in the atmosphere provide a larger gradient
51 over which CO₂ diffuses into the interior airspace of leaves. As a result, most plant
52 types close their stomata in response to increasing CO₂ (the stomatal response), thereby
53 decreasing transpiration per leaf area (Field et al. 1995). In contrast, photosynthetic
54 rates in some cases are limited by access to CO₂, and in those cases more CO₂ can lead
55 to higher rates of photosynthesis, dubbed CO₂ fertilization. This directly impacts
56 photosynthetic rates, with higher photosynthesis (and thus higher stomatal
57 conductance) expected as CO₂ concentrations increase. CO₂ fertilization tends to either
58 have no influence on canopy leaf area or to increase canopy leaf area (Norby and Zak
59 2011; Donohue et al. 2013), which increases transpiration. The physiological effect’s net
60 influence on land evapotranspiration therefore depends on the relative magnitude of
61 these two changes (the stomatal response and the leaf area response), as well as the
62 extent to which vegetation influences land-atmosphere interactions in a given region
63 (Lian et al. 2018). Most Earth system models (ESMs; Swann et al. 2016; Lemordant et
64 al. 2018) and field experiments (Hungate et al. 2002; Leakey et al. 2009) suggest that
65 the stomatal response term dominates in areas with moderate to high leaf area, leading
66 to a net decrease in land evapotranspiration. However, future projections of

67 photosynthetic rates, leaf growth rates, and thus transpiration remain highly uncertain
68 (Friedlingstein et al. 2006; Anav et al. 2013; Piao et al. 2013; Smith et al. 2016; Lian et
69 al. 2018).

70 Physiologically-driven reductions in evapotranspiration can warm local land
71 temperatures directly by decreasing evaporative cooling, as well as indirectly through
72 influences on low level humidity, cloud cover, and precipitation. Recent modeling studies
73 have demonstrated that physiologically-driven decreases in land evapotranspiration can
74 reduce cloud cover by decreasing low level relative humidity (Doutriaux-Boucher et al.
75 2009; Andrews et al. 2011, 2012; Arellano et al. 2012; Lemordant et al. 2018), which
76 amplifies regional physiologically-driven warming. If the leaf area response were to
77 dominate over stomatal responses, the resulting increase in evapotranspiration could
78 decrease land temperatures through these same mechanisms. Kooperman et al. (2018)
79 and Langenbrunner et al. (2019) have also found that physiologically-forced drying of
80 the boundary layer can reduce deep convection and allow for greater advective moisture
81 transport out of lowland forest areas in the lower troposphere, demonstrating that the
82 physiological response not only modulates local surface energy fluxes, but also impacts
83 large scale atmospheric dynamics.

84 In addition to influencing land surface temperature by altering
85 evapotranspiration, the plant physiological response to CO₂ can also influence land
86 surface temperature by altering land surface albedo. CO₂ fertilization generally decreases
87 albedo (thereby increasing temperature) by increasing leaf area and, within dynamic
88 vegetation models, by shifting plant functional types from grasses to trees (Bala et al.
89 2006; Andrews et al. 2019). Expansion of forests in boreal and Arctic regions can result
90 in especially large albedo decreases (Betts 2000; Bala et al. 2006; O'ishi et al. 2009;
91 Andrews et al. 2019) because increases in foliage mask bright snow.

92 The global-scale temperature implications of plants' physiological responses to
93 CO₂ have been long acknowledged. Sellers et al. (1996) were the first to quantify
94 physiologically-driven warming by coupling a biosphere model to an atmosphere model,
95 finding that under a doubling of CO₂ the physiological effect increased global land
96 temperature by about 0.3°C and mean global temperature by about 0.1°C. Since then,
97 multiple modeling studies have demonstrated that the plant physiological response tends
98 to increase land temperatures in most modern ESMs on annual timescales (Betts et al.
99 2007; Andrews et al. 2011; Arora et al. 2013; Swann et al. 2016; Lemordant et al. 2016,
100 2018; Arora et al. 2019) and during heatwaves (Lemordant et al. 2016; Skinner et al.
101 2018; Lemordant and Gentine 2019).

102 Because the physiological effect influences surface temperatures, it is therefore
103 relevant to global-scale metrics of climate sensitivity, such as the equilibrium climate
104 sensitivity (ECS) and transient climate response (TCR). From the perspective of the
105 classical radiative forcing-feedback framework (Gregory et al. 2004; Bony et al. 2006;
106 Roe 2009; Boucher et al. 2013), plants' physiological response to increasing CO₂ can be
107 considered to be a forcing – rather than a feedback – on the climate system because by
108 definition plants are responding to changes in CO₂ rather than to the relatively slow
109 changes in global temperature. However, the timescale over which plants respond to
110 increasing CO₂ ranges from on order seconds to decades. The stomatal response is fast;
111 at the leaf level, stomata respond to changing environmental conditions in less than an
112 hour (Vico et al. 2011), and the timescale of the atmospheric adjustment to the stomatal
113 response occurs on the timescale of a few months (Doutriaux-Boucher et al. 2009;
114 Andrews et al. 2011). Doutriaux-Boucher et al. (2009) have demonstrated that this fast
115 stomatal response rapidly reduces low cloud cover and thereby the cloud radiative effect,
116 which has been shown to be an important contributor to global warming and its
117 uncertainty (Geoffroy et al. 2012). The leaf area and plant distribution responses are

118 slower, occurring on timescales of years to decades (Fisher et al. 2019). Thus, whether
119 the physiological effect will be included in the calculation of radiative forcing depends on
120 the definition used: it would be excluded from the *instantaneous* radiative forcing, which
121 accounts only for the instantaneous impact of CO₂ on the top-of-atmosphere radiation
122 budget; but it would be included in the *effective* radiative forcing, which allows for
123 adjustments to the troposphere, stratosphere, and land surface properties (Sherwood et
124 al. 2015). We will discuss this ambiguity in more detail later, but we focus our analysis
125 on the influence of the physiological effect on the TCR, which is independent of the
126 forcing definition used.

127 Although plants' physiological responses to CO₂ are already embedded in the
128 ESMs used to estimate the TCR, the physiological effect's contribution to this metric
129 has received limited recognition by the climate dynamics community. While studies
130 focusing on carbon cycle feedbacks have quantified physiologically-driven warming
131 across models as part of disentangling carbon-concentration and carbon-climate
132 feedbacks (e.g. Arora et al. 2013, 2019), studies of the physiological contribution to CO₂-
133 forced warming within a climate dynamics framework have been limited to ESMs from a
134 few individual modeling centers (summarized in Table S1 in the online supplement;
135 Sellers et al. 1996; Betts et al. 1997; Cox et al. 1999; Douville et al. 2000; Levis et al.
136 2000; Bala et al. 2006; Betts et al. 2007; Doutriaux-Boucher et al. 2009; Boucher et al.
137 2009; Cao et al. 2009; O'ishi et al. 2009; Cao et al. 2010; Andrews et al. 2011; Pu and
138 Dickinson 2012). Physiology's contribution to the TCR has not been systematically
139 assessed across models and Coupled Model Intercomparison Project (CMIP) phases.

140 Additionally, past studies have not specifically quantified the physiological
141 contribution to the TCR using the same experimental methodology from which the full
142 TCR is calculated. For example, baseline levels of CO₂ have ranged from 280 to 400
143 ppm across experiments (Table S1 in online supplemental material) and the

144 physiological effect's influence on temperature has been analyzed from both abrupt (e.g.
145 Doutriaux-Boucher et al. 2009; Cao et al. 2010; Andrews et al. 2011) and transient
146 (Bala et al. 2006; Boucher et al. 2009) CO₂ perturbations. Modeling studies have also
147 differed in whether they include both the stomatal and leaf area components of the
148 physiological effect or only the stomatal component. While these different experimental
149 designs have provided insights into the mechanisms and timescales of the physiological
150 effect's influence on climate, they do not provide systematic estimates of the full
151 physiological contribution to the TCR across ESMs.

152 The lack of systematic inter-model comparison of the physiological contribution
153 to the TCR is a problematic gap in the existing literature because past work suggests
154 that physiologically-driven transient warming may differ across models. Models disagree
155 both on how plants respond to increasing CO₂ (Friedlingstein et al. 2006; Anav et al.
156 2013; Piao et al. 2013; Smith et al. 2016; Lian et al. 2018) and on how the atmosphere
157 responds to perturbations to the land surface energy budget (Andrews et al. 2009;
158 Devaraju et al. 2018). This suggests that inter-model disagreement about the magnitude
159 of physiologically-driven warming may be an unrecognized contributor to inter-model
160 spread in CO₂-forced warming. Additionally, poor model agreement on the magnitude of
161 physiologically-driven warming would mean that an estimate derived from a single
162 model may not capture the true multi-model mean. To address this gap, we use
163 standardized carbon cycle model simulations from the CMIP phase 5 and 6 archives to
164 quantify (1) the magnitude of the physiological effect's influence on temperature across
165 models, (2) whether trends in the physiological effect contribute to the increase in the
166 TCR noted for many recent models (Andrews et al. 2019; Gettelman et al. 2019; Golaz
167 et al. 2019; Flynn and Mauritsen 2020), (3) the spatial pattern of physiologically-driven
168 temperature changes, (4) how physiological processes contribute to variability in multi-

169 model estimates of the TCR, and (5) the mechanism through which the physiological
170 effect influences temperature.

171

172 **2. Methods**

173 **2.1. CMIP Experiments**

174 As part of CMIP5 and CMIP6, modeling groups performed three concentration-
175 driven experiments (summarized in Table 1) in which CO₂ concentrations increase by 1
176 percent per year from pre-industrial levels (284.3 ppm) to a quadrupling of CO₂ (1144.9
177 ppm), while all other forcings remain at pre-industrial levels. The spatial pattern of
178 vegetation in these simulations comes from the pre-industrial era; this spatial pattern
179 remains constant throughout the simulation except for in land models with dynamic
180 vegetation (see Tables S2 and S3 in online supplemental material), where the
181 distribution of plant functional types changes based on climate and resource availability.
182 In one set of simulations, referred to here as ‘FULL’ (CMIP6 experiment ‘1pctCO2’),
183 both the atmosphere and carbon cycle (on land and in the oceans) experience increasing
184 CO₂ concentrations. Additional experiments conducted as part of the Coupled Climate–
185 Carbon Cycle Model Intercomparison Project (C4MIP; Friedlingstein et al. 2006; Jones
186 et al. 2016) enable us to isolate how much the physiological and radiative effects of CO₂
187 each contribute to surface warming. In one set of C4MIP simulations, referred to here as
188 ‘RAD’ (CMIP6 experiment ‘1pctCO2-rad’), only the atmosphere experiences increasing
189 CO₂ concentrations, while the terrestrial and oceanic carbon cycles experience constant
190 pre-industrial CO₂ concentrations. In another set of C4MIP simulations, referred to here
191 as ‘PHYS’ (CMIP6 experiment ‘1pctCO2-bgc’), the radiative transfer submodels in the
192 atmosphere experience constant pre-industrial CO₂ concentrations, while the land
193 surface and ocean carbon cycle submodels experience the increasing CO₂ concentrations.

194 We use the concentration-driven pre-industrial control experiment (referred to here as
195 ‘PI’, CMIP6 experiment ‘piControl’) as the baseline from which anomalies are taken.

196 **2.2. Models**

197 We analyze output from all ESMs that had uploaded near-surface air
198 temperature monthly data for the FULL, PI, and PHYS and/or RAD experiment to the
199 Earth System Grid by January 29, 2020. This consisted of 8 CMIP5 models and 9
200 CMIP6 models (Table 2). These models all include interactive representations of the
201 carbon cycle; plants in these models respond to increasing CO₂ by changing leaf area,
202 stomatal conductance, and, in some models, the location and distribution of plant
203 functional types (Tables S2 and S3 in online supplemental material). Ocean responses to
204 increasing CO₂ include changes in inorganic and biological carbon cycling, which have
205 negligible direct influences on modeled ocean surface temperature. The only potential
206 direct influences of ocean carbon cycle responses on ocean surface temperatures in the
207 PHYS experiments are through changes in plankton community structure which can
208 alter (1) ocean biogeophysical properties and (2) the emission of gases and particles
209 which influence aerosol formation (Hense et al. 2017). These effects are not represented
210 in most models. When multi-model mean maps are reported, they are calculated after
211 smoothly re-gridding model output to a consistent grid.

212 **2.3. Calculation of the TCR**

213 We calculate the TCR as the change in globally averaged near-surface air
214 temperature during the 20-year window centered on the time of CO₂ doubling (years 61-
215 80 of the simulation where CO₂ concentration increases by 1% per year) relative to pre-
216 industrial CO₂ concentrations. When using the PI experiment as a control, we account
217 for model drift by subtracting the linear trend of PI years 1-140 following Gregory and
218 Forster (2008), where year 1 corresponds to the year at which FULL, RAD, and PHYS

219 were branched from PI. We refer to the physiological and radiative contributions to the
220 full TCR as TCR_{PHYS} and TCR_{RAD} , respectively.

221 We assess whether our estimates of physiologically-driven warming are robust
222 relative to variability in the Earth system by comparing TCR_{PHYS} to the distribution of
223 20-year running mean global temperatures in the full PI control experiments (Figure S1
224 in the online supplemental material). In two of the CMIP6 models evaluated here (BCC-
225 CSM2-MR and CNRM-ESM2-1), large, multidecadal (greater than 20 year) oscillations
226 exist in the PI control (Figure S1 in the online supplemental material; noted in Parsons
227 et al. (In Revision)). The magnitude of these oscillations greatly exceeds the magnitude
228 of the TCR_{PHYS} signal, and thus we cannot confidently quantify the TCR_{PHYS} for these
229 two models. These models' large multidecadal PI oscillations also have implications for
230 TCR_{FULL} , as they suggest that model TCR_{FULL} estimates may be strongly influenced by
231 variability rather than representing the CO_2 -forced warming signal, since for these
232 models smoothing out variability would require an averaging period of greater than 20
233 years.

234 **2.4. Isolating Physiology's Influence on Temperature**

235 We quantify the influence of the physiological effect in two ways: as the
236 difference between the FULL and RAD simulations (FULL-RAD) and as the difference
237 between the PHYS and PI simulations (PHYS-PI). Both represent physiology's
238 influence on the TCR, but FULL-RAD includes any nonlinear interactions between the
239 radiative and physiological effects of increasing CO_2 , while PHYS-PI does not. For
240 example, FULL-RAD would include the interaction between CO_2 fertilization and
241 changes in leaf area (quantified as the leaf area index, LAI) induced by RAD-driven
242 warming. We focus on the FULL-RAD methodology in the main text because it
243 emphasizes how much the physiological effect changes climate relative to what models
244 would otherwise show from radiative forcing alone. Because FULL and RAD branch

245 from the same point of the PI simulation, FULL-RAD also avoids issues related to drift
246 in the PI control. There is some nonlinearity between the radiative and physiological
247 effects of CO₂, but there is poor model agreement on the sign and spatial pattern of the
248 interaction term (Figures S2 and S3 in the online supplemental material).

249 **2.5. Partitioning Physiological Influences on Evapotranspiration**

250 We partition the total physiologically-driven change in land evapotranspiration
251 into its component physiological drivers according to Equation 1, where the four terms
252 on the right-hand side indicate the land evapotranspiration change due to (1) changes in
253 leaf area, (2) changes in stomatal conductance (approximated as changes in
254 transpiration per leaf area), (3) interactions between changes in stomatal conductance
255 and changes in leaf area, and (4) changes in land evaporation. The derivation of
256 Equation 1 is included in the online supplemental material.

257

$$\Delta ET = \left(\frac{T}{L}\right)_{RAD} (\Delta L) + L_{RAD} \left(\Delta \frac{T}{L}\right) + \left(\Delta \frac{T}{L}\right) (\Delta L) + \Delta E \quad \text{Equation 1}$$

258 where ET = evapotranspiration (mm/day); T = transpiration (mm/day); L = leaf area
259 index (unitless); and E = evaporation (mm/day). The RAD subscript indicates the
260 value from the RAD experiment, and Δ indicates the physiologically-driven change, as
261 calculated from FULL-RAD.

262

263 **3. Results and Discussion**

264 **3.1. Physiology's Contribution to the TCR**

265 The radiative effect of CO₂ is, unsurprisingly, the dominant contributor to the
266 TCR. However, we also find that the physiological response to increased CO₂ has a non-
267 negligible secondary contribution to the TCR in many CMIP5 and CMIP6 models. In
268 CMIP6 models, the physiological effect contributes about 0.11°C (standard deviation:

269 0.10°C; range: 0.02 - 0.29°C) to the TCR, corresponding to 5.2% of the full TCR
270 (standard deviation: 4.1%; range: 1.4 - 13.9%) (Figure 1a). For a few CMIP6 models
271 (especially UKESM1-0-LL and CESM2), the physiological contribution to warming is
272 quite large, accounting for over 10% of the total TCR. In CMIP5 models (note that a
273 different subset of modeling centers have the necessary CMIP5 model simulations; see
274 Table 2), the physiological effect contributes 0.14°C (standard deviation: 0.16°C; range:
275 0.00 - 0.51°C) to the TCR, corresponding to 6.6% of the full TCR (standard deviation:
276 6.3%; range: 0.1 - 20.1%).

277 When comparing the same subset of six models for which we have model output
278 from both CMIP phases, physiologically-driven warming is comparable in CMIP5 and
279 CMIP6. From CMIP5 to CMIP6, the mean TCR_{PHYS} across these models remained
280 roughly constant (Table 2). TCR_{PHYS} increased for 4 of 6 models (Table 2; Figure 1b),
281 but notably decreased for the model with the highest TCR_{PHYS} in CMIP5 (the Met
282 Office Hadley Centre model, which is HadGEM2-ES in CMIP5 and UKESM1-0-LL in
283 CMIP6). This suggests that the increases in TCR_{FULL} from CMIP5 to CMIP6 noted for
284 many recent models (Andrews et al. 2019; Gettelman et al. 2019; Golaz et al. 2019;
285 Flynn and Mauritsen 2020) were driven primarily by increases in TCR_{RAD} rather than
286 TCR_{PHYS} . Physiology's relative contribution to the TCR decreased in most models
287 (Figure 1a, Table 2), due to many CMIP6 models' increased values of TCR_{RAD} .

288 The multi-model mean TCR_{PHYS} values reported here are within the range of
289 estimates from other studies (summarized in Table S1 in online supplemental material),
290 but on the low side of this range for two reasons. Firstly, this may relate to publication
291 bias: of the eleven modeling centers included in this analysis, the only two modeling
292 centers that had previously published CMIP5 estimates of physiologically-driven
293 warming at $2xCO_2$ have above average TCR_{PHYS} . Our study is the first to compare
294 TCR_{PHYS} across models, and the fact that the existing literature did not capture the full

295 spread in TCR_{PHYS} across models underscores the importance of a multi-model
296 approach. A second reason that our multi-model estimate of TCR_{PHYS} is on the low side
297 of previous estimates results from the fact that many previous studies isolated the effect
298 of the stomatal response on near-surface temperatures rather than the net effect of both
299 the stomatal and leaf area response (Table S1 in online supplemental material); we
300 expect a larger temperature increase from the stomatal response alone than from the
301 combined stomatal and leaf area responses because the leaf area response counteracts
302 the stomatal response's influence on evapotranspiration.

303 The global mean TCR_{PHYS} signal is small in comparison to TCR_{FULL} , and it is
304 statistically significant relative to the pre-industrial control for only 4 of 9 CMIP6 and 5
305 of 8 CMIP5 models at $2\times\text{CO}_2$ (Table S4 in online supplemental material). However, the
306 physiologically-driven warming signal increases with increasing CO_2 concentration,
307 reaching a mean of 0.20°C (standard deviation: 0.12°C ; range: $0.03 - 0.45^\circ\text{C}$) by $4\times\text{CO}_2$
308 and emerging from the noise (Figure 1b). By $4\times\text{CO}_2$, physiologically-driven warming is
309 statistically significant for 6 of 9 CMIP6 and 7 of 8 CMIP5 models (Table S4 in online
310 supplemental material). The three CMIP6 models that are not statistically significant
311 by $4\times\text{CO}_2$ (CNRM-ESM2-1, BCC-CSM2-MR, and IPSL-CM6A-LR) are the three
312 models with the most variability in the PI control of all the CMIP5 and CMIP6 models
313 we analyze. The significant physiologically-driven warming at higher CO_2
314 concentrations, inter-model agreement in the sign of TCR_{PHYS} , and consistent spatial
315 pattern of warming (detailed in section 3.2) gives us confidence that we are detecting a
316 real physiologically-driven signal and not just picking up internal variability. However,
317 internal variability is a large source of uncertainty in quantifying TCR_{PHYS} (Figure 1b),
318 and this uncertainty is intrinsically included in estimates of TCR_{FULL} . Integration of a
319 large-ensembles approach into the next C4MIP is necessary to address this issue and to

320 reduce uncertainties in the TCR in future work. This could be done through integrating
321 a requirement for a minimum number of initial condition ensembles in the experiment.

322 **3.2. Spatial Pattern of Physiologically-Driven Warming**

323 The physiological effect only directly influences land surface properties, and thus
324 the largest warming driven by the physiological effect occurs over land. In CMIP6
325 models, the physiological effect results in a land mean warming of 0.21°C at 2xCO₂ and
326 0.41°C at 4xCO₂, relative to a corresponding mean ocean warming of 0.07°C and 0.13°C
327 respectively (Figure 2a). Physiologically-driven warming over land is also statistically
328 significant for more ESMs by 2xCO₂ than it is for the global mean (Table S4 in online
329 supplemental material). Because most models do not have any mechanism for the
330 physiological effect of CO₂ to directly warm the oceans, the modelled physiologically-
331 driven warming over oceans must be the result of remote, land driven warming. The
332 spatial pattern of physiologically-driven warming that we find is consistent with other
333 studies, which also show the greatest warming over land and modest ocean warming
334 (Table S1 in online supplemental material).

335 The greatest mean physiologically-driven warming occurs over boreal forests and
336 non-glaciated high-latitude land, followed by temperate and tropical forested regions.
337 The agreement across models is reasonably high - at least 6 of 9 CMIP6 models agree
338 that the physiological effect results in warming in these three biomes at 2xCO₂, and 8 of
339 9 CMIP6 models show warming in these biomes at 4xCO₂ (Figures S4 and S5). Relative
340 to radiatively-driven warming, physiology also contributes more to land warming than
341 ocean warming, with physiological forcing constituting a mean 7.3% of total CO₂-forced
342 land warming at 2xCO₂ compared to 4.2% of ocean warming (Figure 2b). The
343 physiological effect therefore amplifies the land/ocean warming contrast: while land
344 warms a mean 1.57 times more than ocean in RAD for CMIP6, the mean land/ocean
345 warming contrast in FULL is 1.62, due to the addition of the physiological effect (Figure

346 3). This physiologically-driven enhancement of the land/ocean warming contrast was
347 previously demonstrated for Met Office Hadley Centre models (Joshi et al. 2008; Dong
348 et al. 2009), and we show here that this warming contrast is robust across most CMIP
349 models (Figure 3).

350 The larger absolute and relative physiologically-driven warming over non-
351 glaciated land is consistent with the physiological effect directly influencing land surface
352 properties in regions with plant cover, while influencing glaciated land and oceans only
353 indirectly through changes in heat transport, clouds, and other aspects of climate
354 dynamics. Though the remote influence of physiological forcing on oceans and glaciated
355 land is relatively modest, most models (8 of 9) agree that the physiological effect results
356 in mean warming of near-surface oceanic air and ocean surface layers. The regions of the
357 most robust physiologically-driven oceanic warming across models are the western North
358 Atlantic, equatorial Pacific, equatorial Indian Ocean, and high latitude Pacific.

359 Byrne and O’Gorman (2018) suggest that increases in the near surface land-ocean
360 temperature contrast are causally driven by temperature change over the ocean.
361 However, the physiologically-driven enhanced land-ocean contrast, where the only initial
362 difference is over the land surface, shows that land surface processes can also initiate the
363 feedback loop of decreasing relative humidity over land leading to a larger increase in
364 temperature over land relative to over ocean. The potential to initiate this loop through
365 land processes is noted by Byrne and O’Gorman (2016), and we further emphasize that
366 point here. It is important to acknowledge the physiological effect’s greater relative
367 contribution to land warming because land warming (rather than global mean warming)
368 is the relevant metric for many societal climate impacts.

369 **3.3. Physiology’s Contribution to Uncertainty in CO₂-Forced** 370 **Warming**

371 The magnitude of global physiologically-driven warming varies significantly
372 across models (Figures 1 and 4) and this uncertainty contributes to the inter-model
373 spread of TCR estimates. In the CMIP6 models analyzed here, the radiative effect alone
374 explains about 89% of the standard deviation and 91% of the inter-model range in the
375 TCR (Figure 5), with the physiological effect contributing the remaining 11% and 9%,
376 respectively. The physiological effect contributes more to uncertainty in CO₂-forced
377 warming over land. Averaged across all non-glaciated land, the physiological effect
378 explains about 16% of the standard deviation and 18% of the inter-model range mean
379 land warming at 2xCO₂ in CMIP6 (Figure 5). In some highly forested land regions
380 (tropical Africa, southeastern South America, and the southeastern United States),
381 inter-model disagreement in local warming at 2xCO₂ is driven by approximately equal
382 contributions of uncertainty from physiologically- and radiatively-forced warming
383 (Figure 6). These results suggest that the physiological effect is a non-negligible
384 contributor to inter-model spread in the TCR and regional CO₂-forced warming.
385 However, some of these pre-industrial forested regions, especially southeastern South
386 America, are largely deforested in the present day, which means that in scenario-based
387 future projections the physiological effect may contribute less to uncertainty in these
388 regions than Figure 6 implies.

389 A limitation of this study is that the C4MIP model output necessary to
390 disentangle physiologically- and radiatively-forced warming is only available for about a
391 quarter of the models for which we can estimate the full TCR (9 of 34 for CMIP6 and 8
392 of 30 for CMIP5). We therefore cannot quantify TCR_{PHYS}, or the physiological
393 contribution to uncertainty in the TCR, for the remaining CMIP models. Future work
394 could further leverage C4MIP model output to assess whether signatures of

395 physiologically-driven warming (such as seasonal variations in the CO₂-forced change of
396 the diurnal temperature range; Bounoua et al. 1999; Collatz et al. 2000; Leeuwen et al.
397 2011) could be used to estimate the physiological contributions to mean warming from
398 the FULL experiments alone.

399 **3.4. Mechanism of Physiologically-Driven Warming**

400 ***3.4.1. Land Mechanism***

401 The physiological effect increases near-surface air temperatures over land by
402 modifying surface properties which modulate terrestrial energy fluxes (Laguë et al.
403 2019). This occurs through (1) changes in the partitioning between surface turbulent
404 fluxes resulting from physiological influences on evapotranspiration, (2) radiative
405 changes due to physiologically-driven changes in albedo, cloud cover, and column water
406 vapor, and (3) changes in surface roughness resulting from changes in leaf area and
407 vegetation distribution.

408 In most models, plants' response to CO₂ causes a net decrease in mean land
409 evapotranspiration, especially in the tropics (Figure 7), indicating that stomatal closure
410 decreases evapotranspiration by enough to offset increases in evapotranspiration from
411 increased leaf area, though the magnitude and sign of evapotranspiration change does
412 vary spatially across models. In the CMIP6 multi-model mean at 2xCO₂, changes in
413 stomatal conductance (approximated by the change in transpiration per leaf area)
414 decreases global land evapotranspiration by 0.14 mm/day (standard deviation: 0.08
415 mm/day; range: 0.02-0.27 mm/day), global leaf area changes increase evapotranspiration
416 by 0.19 mm/day (standard deviation: 0.15 mm/day; range: 0.00-0.52 mm/day), and the
417 interaction between changes in stomatal conductance and leaf area decreases
418 evapotranspiration by an additional 0.07 mm/day (standard deviation: 0.08 mm/day;
419 range: 0.00-0.29 mm/day; Figure 8). Land evaporation changes minimally (0.00
420 mm/day; standard deviation: 0.03 mm/day; range: -0.06 - +0.05 mm/day; Figure 8). In

421 the multi-model mean, the net effect of these physiological responses is a decrease in
422 evapotranspiration, with the largest and most robust decrease in the tropics (Figures 7,
423 8, and 9). This physiologically-driven decrease in evapotranspiration due to increased
424 CO₂ has previously been documented for CMIP5 models (Swann et al. 2016; Lemordant
425 et al. 2018), and holds for the new CMIP6 models analyzed here. Under constant net
426 radiation at the surface, this physiologically-driven decrease in evapotranspiration
427 results in more energy leaving the land surface through sensible heating (Figure 9),
428 thereby increasing near-surface air temperatures.

429 The physiological effect also increases surface and near-surface temperatures by
430 increasing the net radiation reaching the surface. Net shortwave radiation on land
431 increases primarily through albedo decreases and changes in cloud cover (Figure 9).
432 Albedo decreases primarily in high latitudes (Figure 7), due to both increases in leaf
433 area and decreases in snow cover due to increased temperatures. Consistent with
434 previous studies (Doutriaux-Boucher et al. 2009; Andrews et al. 2011, 2012; Arellano et
435 al. 2012; Lemordant et al. 2018), downwelling shortwave radiation (SW_{down}) reaching
436 the surface also increases as a consequence of decreases in cloud cover (especially in
437 Northern Hemisphere mid- and high-latitudes and over the northeastern Amazon;
438 Figure 9), which are driven both by decreases in relative humidity from physiologically-
439 forced reductions in evapotranspiration and by increases in air temperatures. Most
440 models show negligible mean changes in clear-sky SW_{down} (which could be modified by
441 changes in water vapor and aerosols), with the exception of UKESM1-0-LL and
442 CanESM5, which show slight decreases in SW_{down} . This result differs from CMIP5, in
443 which the Hadley Centre model was the only model to show physiologically-driven
444 changes in clear-sky SW_{down} , which increased due to vegetation's influence on dust
445 optical depth (Andrews et al. 2012).

446 The physiological effect also influences surface net longwave radiation (Figure 9)
447 through changes in surface and boundary layer temperatures, cloud cover, atmospheric
448 column water vapor, and the partitioning of surface energy fluxes. Outgoing longwave
449 radiation from the land surface (LW_{up}) increases with increasing surface temperature
450 through the Planck feedback. Warming of the boundary layer (driven by both increased
451 sensible heating and by longwave radiation associated with surface warming) increases
452 downward longwave radiation at the land surface (LW_{down}), partially offsetting the
453 increase in LW_{up} (Vargas Zeppetello et al. 2019). Physiologically-driven decreases in
454 atmospheric water vapor (which is a strong greenhouse gas) decrease LW_{down} , as do
455 cloud changes resulting from reduced land evapotranspiration. The net effect of all of
456 these processes generally results in a decrease of net longwave radiation over most
457 vegetated land.

458 ***3.4.2. Ocean Mechanism***

459 Because most models do not have any mechanism for the physiological effect of
460 CO_2 to directly warm the oceans, the modelled physiologically-driven oceanic warming
461 must be the result of remote, land-driven warming. The physiological effect on land can
462 alter ocean temperatures through (1) advection of continental air that has been directly
463 influenced by changes in land surface properties (e.g. changes in air temperature or
464 moisture content) and (2) changes in atmospheric or oceanic circulation. The fact that
465 the most robust oceanic warming regions are downwind of warming land regions
466 suggests that advection of warm continental air is contributing to oceanic warming.
467 Cloud cover over oceans also decreases in some regions that are downwind of land,
468 particularly in the North Atlantic, increasing ocean temperatures by increasing net
469 radiation (Figure 9).

470 Teleconnections likely also contribute to ocean warming, based on past work
471 indicating that changes in large-scale atmospheric circulation can be induced by

472 physiological forcing (Kooperman et al. 2018; Langenbrunner et al. 2019) or other
473 changes in land surface properties (Swann et al. 2012, 2014; Devaraju et al. 2015; Laguë
474 and Swann 2016; Devaraju et al. 2018). Additionally, the physiological effect has the
475 potential to induce changes in ocean circulation (e.g. Diffenbaugh et al. 2004). In
476 particular, the pattern of physiologically-driven oceanic warming in the North Atlantic
477 is consistent with a weakening of the Atlantic Meridional Overturning Circulation
478 (AMOC; e.g. Marshall et al. 2015; Caesar et al. 2018). A potential mechanism is that
479 warming of the air advected off the North American continent would reduce the flux of
480 heat from the ocean to the atmosphere in the subpolar North Atlantic, decreasing deep
481 convection.

482 While the C4MIP experimental design does not enable us to directly quantify the
483 relative contributions of advection and circulation changes to oceanic warming,
484 exploration of the links between land surface perturbations and ocean temperatures
485 merits further research. Recognizing the oceanic component of physiologically-driven
486 warming is important because it constitutes about half of TCR_{PHYS} – even though the
487 magnitude of physiologically-driven oceanic warming is much smaller than land warming
488 on a per area basis, the TCR is a global-scale metric and ocean constitutes about 70% of
489 the Earth’s surface area.

490

491 **4. Conclusions and Implications**

492 **4.1. Magnitude of TCR_{PHYS}**

493 The biological and ecological processes governing canopy leaf area and stomatal
494 conductance are often considered to exist squarely in the domain of carbon cycle
495 feedbacks (i.e. they impact the climate system through their influence on CO_2
496 concentrations themselves). Our analysis demonstrates that these terrestrial carbon

497 cycle processes are also embedded in global climate sensitivity metrics like the TCR
498 through plants' impact on land surface properties and surface energy fluxes.

499 We quantified the plant physiological effect's small but significant influence on
500 CO₂-forced temperature changes, finding that at 2xCO₂ the physiological effect
501 contributes about 0.11°C (5.2%) to the TCR and leads to about 0.21°C of warming over
502 non-glaciated land. To put our results into context, the physiological contribution to the
503 TCR is the same order of magnitude as the surface albedo feedback's contribution to
504 equilibrium warming (8% of the ECS as quantified for CMIP5 models by Vial et al.
505 2013). Recognizing this physiological component of CO₂ forcing is necessary for
506 understanding forcing differences across greenhouse gases (e.g. CH₄ does not have added
507 warming from physiology). While the contribution of the physiological effect can be up
508 to 20% of the total TCR in some CMIP5 models, changes in the representation of plant
509 physiology do not appear to be a major driver of the increase in the TCR observed from
510 CMIP5 to CMIP6.

511 **4.2. Physiology's Role in Forcing, Feedbacks, and ECS**

512 The effective radiative forcing is commonly expressed as a change in net top-of-
513 atmosphere (TOA) radiation following CO₂-driven adjustments in tropospheric and
514 stratospheric temperatures, water vapor, clouds, and surface properties, prior to any
515 global-mean surface temperature change (e.g. Boucher et al. 2013; Sherwood et al.
516 2015). In practice, it is often calculated using simulations in which CO₂ is increased
517 while sea-surface temperatures (SSTs) are prescribed to be fixed at pre-industrial values,
518 with some studies estimating and removing the TOA radiative response to land
519 warming when calculating the forcing value (Hansen et al. 2005; Vial et al. 2013; Tang
520 et al. 2019). Meanwhile, radiative feedbacks are traditionally defined by the change in
521 net TOA radiation for a given change in global-mean surface temperature (Bony et al.
522 2006; Roe 2009).

523 The physiological response of plants to increasing CO₂ poses a challenge to this
524 radiative forcing–feedback paradigm. On the one hand, plants respond directly to the
525 atmospheric CO₂ concentration, suggesting that the physiological effect should be
526 classified as part of the forcing. However, because this direct physiological response of
527 plants to CO₂ induces changes in surface temperature (even in the absence of the
528 radiative effects of CO₂ changes), the TOA radiative response to these changes could
529 also be classified as part of the feedback. Meanwhile, temperature-driven changes in
530 vegetation distribution and leaf area that influence land surface albedo and
531 evapotranspiration should clearly be classified as feedbacks. While it is unclear to us
532 how best to interpret the physiological effect in terms of the forcing–feedback paradigm,
533 the distinction does not impact the results presented here because of our results’ focus
534 on the TCR instead of forcing or feedbacks separately.

535 However, understanding of the role of the physiological effect in TCR and ECS
536 uncertainty would benefit from greater clarity on whether it should be treated as a
537 forcing or feedback. Indeed, recent work suggests that the TCR may be more sensitive
538 to uncertainty in CO₂ radiative forcing than to uncertainty in radiative feedbacks
539 (Lutsko and Popp 2019), but that the ECS is more sensitive to uncertainty in radiative
540 feedbacks (Geoffroy et al. 2012). Thus, while the results here suggest that the
541 physiological effect will act to increase the ECS and its uncertainty – as it has for the
542 TCR – we cannot currently quantify the magnitude of the effect on the ECS in the
543 CMIP5 or CMIP6 ensembles. Additional RAD and PHYS simulations for abrupt CO₂
544 quadrupling, using both fixed SSTs¹ to be able to quantify the effective radiative forcing

¹ For example, the CMIP6 Cloud Feedback Model Intercomparison Project (CFMIP; Webb et al. 2017) tier 2 experiment piSST-4xCO2-rad, in which SSTs are fixed at pre-industrial levels and only the radiation scheme (and not the vegetation scheme) experience an abrupt quadrupling of CO₂

545 and coupled model simulations to be able to estimate ECS, would be valuable in this
546 regard.

547 **4.3. Broad Implications of Carbon Cycle Uncertainty**

548 While we report physiology's mean contribution to warming, we especially
549 emphasize our finding that uncertainty in terrestrial carbon cycle processes contributes
550 to uncertainty in CO₂-forced warming. The spread in the magnitude of physiologically-
551 driven warming across CMIP6 models represents real scientific uncertainty, as there are
552 limited observational constraints to suggest that either the high or low extremes of
553 modeled physiological responses of stomatal conductance, leaf area, and resulting
554 evapotranspiration are within expectations (Medlyn et al. 2011; De Kauwe et al. 2013;
555 Schimel et al. 2015).

556 It is also possible that ESMs do not probe the full scientific uncertainty
557 surrounding plants' responses to CO₂, as models may contain systematic biases. For
558 example, many models represent stomatal conductance using the same key parameters
559 (e.g. the same slope constant in the Ball-Berry (1987) stomatal conductance model or
560 the g_1 fitted parameter in the Medlyn (2011) model) to govern how stomatal
561 conductance responds to increasing CO₂, despite the wide variation in these parameters
562 across and within plant functional types (Lin et al. 2015; Wolz et al. 2017). Similarly,
563 some studies suggest (e.g. Smith et al. 2016) that ESMs systematically overestimate the
564 leaf area increases resulting from CO₂ fertilization, which would mean that models
565 overestimate physiologically-driven albedo decreases and underestimate physiologically-
566 driven evapotranspiration decreases. We would expect this to result in a true
567 physiologically-forced temperature change that is smaller than models suggest at high
568 latitudes (where albedo matters more) and larger than models suggest at low latitudes
569 (where ET matters more). Furthermore, Green et al. (2017) suggest that ESMs may

570 systematically underestimate some feedbacks between land biosphere changes and the
571 atmosphere.

572 On the one hand, acknowledging the physiological contribution to uncertainty in
573 modeled CO₂-forced warming suggests that models agree more on the magnitude of
574 radiatively forced warming than the prevailing narrative implies. For atmospheric
575 dynamicists most interested in purely radiatively-driven processes, these findings
576 therefore motivate more deliberate consideration of plant functioning in experimental
577 designs; RAD simulations may be more appropriate than FULL simulations for some
578 climate dynamics questions. On the other hand, acknowledging the physiological
579 contribution means that reducing uncertainty in the true, full TCR requires reducing
580 uncertainty in land surface processes which are especially difficult to constrain. From
581 this perspective, these findings provide a new motivation for further experimental
582 studies to reduce uncertainty in terrestrial carbon cycle processes. For example, we
583 identify that plants' responses to CO₂ are a major driver of uncertainty in transient
584 warming in tropical Africa, and no free-air CO₂ enrichment (FACE) experiments exist
585 in tropical forests to constrain uncertainty in how those ecosystems will respond to
586 increasing CO₂. Carbon cycle uncertainty is not limited to the carbon cycle, and
587 reducing uncertainty in plants' response to CO₂ will improve our understanding of
588 physiological warming, thereby reducing overall uncertainty in the total TCR.

589

590 **5. Data and Code Availability**

591 The majority of model output data used in this study are available in the
592 publicly accessible Earth System Grid Federation (ESGF) repository at [https://esgf-](https://esgf-node.llnl.gov/projects/esgf-llnl/)
593 [node.llnl.gov/projects/esgf-llnl/](https://esgf-node.llnl.gov/projects/esgf-llnl/). Model output from the CESM2 RAD experiment is not
594 yet available on the ESGF repository and is stored on data servers at the National

595 Center for Atmospheric Research. The code used for this study is available from the
596 corresponding author upon request.

597

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611

612 **7. References**

613

614 Anav, A., and Coauthors, 2013: Evaluating the Land and Ocean Components of the
615 Global Carbon Cycle in the CMIP5 Earth System Models. *J. Clim.*, **26**,
616 <https://doi.org/10.1175/JCLI-D-12-00417.1>.

617 Andrews, T., P. M. Forster, and J. M. Gregory, 2009: A Surface Energy Perspective on
618 Climate Change. *J. Clim.*, **22**, 2557–2570,
619 <https://doi.org/10.1175/2008JCLI2759.1>.

620 —, M. Doutriaux-Boucher, O. Boucher, and P. M. Forster, 2011: A regional and
621 global analysis of carbon dioxide physiological forcing and its impact on climate.
622 *Clim. Dyn.*, **36**, 783–792, <https://doi.org/10.1007/s00382-010-0742-1>.

623 —, M. A. Ringer, M. Doutriaux-Boucher, M. J. Webb, and W. J. Collins, 2012:
624 Sensitivity of an Earth system climate model to idealized radiative forcing.
625 *Geophys. Res. Lett.*, **39**, <https://doi.org/10.1029/2012GL051942>.

626 —, and Coauthors, 2019: Forcings, Feedbacks, and Climate Sensitivity in HadGEM3-
627 GC3.1 and UKESM1. *J. Adv. Model. Earth Syst.*, **n/a**,
628 <https://doi.org/10.1029/2019MS001866>.

629 Arellano, J. V.-G. de, C. C. van Heerwaarden, and J. Lelieveld, 2012: Modelled
630 suppression of boundary-layer clouds by plants in a CO₂-rich atmosphere. *Nat.*
631 *Geosci.*, **5**, 701–704, <https://doi.org/10.1038/ngeo1554>.

632 Arora, V. K., and Coauthors, 2013: Carbon-Concentration and Carbon-Climate
633 Feedbacks in CMIP5 Earth System Models. *J. Clim.*, **26**, 5289–5314,
634 <https://doi.org/10.1175/JCLI-D-12-00494.1>.

635 —, and Coauthors, 2019: Carbon-concentration and carbon-climate feedbacks in
636 CMIP6 models, and their comparison to CMIP5 models. *Biogeosciences Discuss.*,
637 <https://doi.org/10.5194/bg-2019-473>.

638 Bala, G., K. Caldeira, A. Mirin, M. Wickett, C. Delire, and T. J. Phillips, 2006:
639 Biogeophysical effects of CO₂ fertilization on global climate. *Tellus B*, **58**, 620–
640 627, <https://doi.org/10.1111/j.1600-0889.2006.00210.x>.

641 Ball, J. T., I. E. Woodrow, and J. A. Berry, 1987: A Model Predicting Stomatal
642 Conductance and its Contribution to the Control of Photosynthesis under

643 Different Environmental Conditions. *Progress in Photosynthesis Research*, J.
644 Biggins, Ed., Springer Netherlands, 221–224.

645 Betts, R. A., 2000: Offset of the potential carbon sink from boreal forestation by
646 decreases in surface albedo. *Nature*, **408**, 187–190,
647 <https://doi.org/10.1038/35041545>.

648 ———, P. M. Cox, S. E. Lee, and F. I. Woodward, 1997: Contrasting physiological and
649 structural vegetation feedbacks in climate change simulations. *Nature*, **387**, 796–
650 799, <https://doi.org/10.1038/42924>.

651 ———, and Coauthors, 2007: Projected increase in continental runoff due to plant
652 responses to increasing carbon dioxide. *Nature*, **448**, 1037–1041,
653 <https://doi.org/10.1038/nature06045>.

654 Bony, S., and Coauthors, 2006: How Well Do We Understand and Evaluate Climate
655 Change Feedback Processes? *J. Clim.*, **19**, 3445–3482,
656 <https://doi.org/10.1175/JCLI3819.1>.

657 Boucher, O., A. Jones, and R. A. Betts, 2009: Climate response to the physiological
658 impact of carbon dioxide on plants in the Met Office Unified Model HadCM3.
659 *Clim. Dyn.*, **32**, 237–249, <https://doi.org/10.1007/s00382-008-0459-6>.

660 ———, and Coauthors, 2013: Clouds and aerosols. *Climate change 2013: the physical
661 science basis. Contribution of Working Group I to the Fifth Assessment Report
662 of the Intergovernmental Panel on Climate Change*.

663 Bounoua, L., and Coauthors, 1999: Interactions between Vegetation and Climate:
664 Radiative and Physiological Effects of Doubled Atmospheric CO₂. *J. Clim.*, **12**,
665 309–324, [https://doi.org/10.1175/1520-0442\(1999\)012<0309:IBVACR>2.0.CO;2](https://doi.org/10.1175/1520-0442(1999)012<0309:IBVACR>2.0.CO;2).

666 Byrne, M. P., and P. A. O’Gorman, 2016: Understanding Decreases in Land Relative
667 Humidity with Global Warming: Conceptual Model and GCM Simulations. *J.*
668 *Clim.*, **29**, 9045–9061, <https://doi.org/10.1175/JCLI-D-16-0351.1>.

669 ———, and ———, 2018: Trends in continental temperature and humidity directly linked to
670 ocean warming. *Proc. Natl. Acad. Sci.*, **115**, 4863–4868,
671 <https://doi.org/10.1073/pnas.1722312115>.

672 Caesar, L., S. Rahmstorf, A. Robinson, G. Feulner, and V. Saba, 2018: Observed
673 fingerprint of a weakening Atlantic Ocean overturning circulation. *Nature*, **556**,
674 191–196, <https://doi.org/10.1038/s41586-018-0006-5>.

675 Cao, L., G. Bala, K. Caldeira, R. Nemani, and G. Ban-Weiss, 2009: Climate response to
676 physiological forcing of carbon dioxide simulated by the coupled Community
677 Atmosphere Model (CAM3.1) and Community Land Model (CLM3.0). *Geophys.*
678 *Res. Lett.*, **36**, <https://doi.org/10.1029/2009GL037724>.

679 ———, ———, ———, ———, and G. Ban-Weiss, 2010: Importance of carbon dioxide
680 physiological forcing to future climate change. *Proc. Natl. Acad. Sci.*, **107**, 9513–
681 9518, <https://doi.org/10.1073/pnas.0913000107>.

682 Collatz, G. J., L. Bounoua, S. O. Los, D. A. Randall, I. Y. Fung, and P. J. Sellers, 2000:
683 A mechanism for the influence of vegetation on the response of the diurnal
684 temperature range to changing climate. *Geophys. Res. Lett.*, **27**, 3381–3384,
685 <https://doi.org/10.1029/1999GL010947>.

686 Cox, P. M., R. A. Betts, C. B. Bunton, R. L. H. Essery, P. R. Rowntree, and J. Smith,
687 1999: The impact of new land surface physics on the GCM simulation of climate

688 and climate sensitivity. *Clim. Dyn.*, **15**, 183–203,
689 <https://doi.org/10.1007/s003820050276>.

690 De Kauwe, M. G., and Coauthors, 2013: Forest water use and water use efficiency at
691 elevated CO₂: a model-data intercomparison at two contrasting temperate forest
692 FACE sites. *Glob. Change Biol.*, **19**, 1759–1779,
693 <https://doi.org/10.1111/gcb.12164>.

694 Devaraju, N., G. Bala, and A. Modak, 2015: Effects of large-scale deforestation on
695 precipitation in the monsoon regions: Remote versus local effects. *Proc. Natl.
696 Acad. Sci.*, **112**, 3257–3262, <https://doi.org/10.1073/pnas.1423439112>.

697 ———, N. de Noblet-Ducoudré, B. Quesada, and G. Bala, 2018: Quantifying the Relative
698 Importance of Direct and Indirect Biophysical Effects of Deforestation on Surface
699 Temperature and Teleconnections. *J. Clim.*, **31**, 3811–3829,
700 <https://doi.org/10.1175/JCLI-D-17-0563.1>.

701 Diffenbaugh, N. S., M. A. Snyder, and L. C. Sloan, 2004: Could CO₂-induced land-cover
702 feedbacks alter near-shore upwelling regimes? *Proc. Natl. Acad. Sci.*, **101**, 27–32,
703 <https://doi.org/10.1073/pnas.0305746101>.

704 Dong, B., J. M. Gregory, and R. T. Sutton, 2009: Understanding Land–Sea Warming
705 Contrast in Response to Increasing Greenhouse Gases. Part I: Transient
706 Adjustment. *J. Clim.*, **22**, 3079–3097, <https://doi.org/10.1175/2009JCLI2652.1>.

707 Donohue, R. J., M. L. Roderick, T. R. McVicar, and G. D. Farquhar, 2013: Impact of
708 CO₂ fertilization on maximum foliage cover across the globe’s warm, arid
709 environments. *Geophys. Res. Lett.*, **40**, 3031–3035,
710 <https://doi.org/10.1002/grl.50563>.

711 Doutriaux-Boucher, M., M. J. Webb, J. M. Gregory, and O. Boucher, 2009: Carbon
712 dioxide induced stomatal closure increases radiative forcing via a rapid reduction
713 in low cloud. *Geophys. Res. Lett.*, **36**, <https://doi.org/10.1029/2008GL036273>.

714 Douville, H., S. Planton, J.-F. Royer, D. B. Stephenson, S. Tyteca, L. Kergoat, S.
715 Lafont, and R. A. Betts, 2000: Importance of vegetation feedbacks in doubled-
716 CO₂ climate experiments. *J. Geophys. Res. Atmospheres*, **105**, 14841–14861,
717 <https://doi.org/10.1029/1999JD901086>.

718 Field, C. B., R. B. Jackson, and H. A. Mooney, 1995: Stomatal responses to increased
719 CO₂: implications from the plant to the global scale. *Plant Cell Environ.*, **18**,
720 1214–1225, <https://doi.org/10.1111/j.1365-3040.1995.tb00630.x>.

721 Fisher, R. A., and Coauthors, 2019: Parametric Controls on Vegetation Responses to
722 Biogeochemical Forcing in the CLM5. *J. Adv. Model. Earth Syst.*,
723 <https://doi.org/10.1029/2019MS001609>.

724 Flynn, C. M., and T. Mauritsen, 2020: On the Climate Sensitivity and Historical
725 Warming Evolution in Recent Coupled Model Ensembles. *Atmospheric Chem.*
726 *Phys. Discuss.*, <https://doi.org/10.5194/acp-2019-1175>.

727 Friedlingstein, P., and Coauthors, 2006: Climate–Carbon Cycle Feedback Analysis:
728 Results from the C4MIP Model Intercomparison. *J. Clim.*, **19**, 3337–3353,
729 <https://doi.org/10.1175/JCLI3800.1>.

730 Geoffroy, O., D. Saint-Martin, and A. Ribes, 2012: Quantifying the sources of spread in
731 climate change experiments. *Geophys. Res. Lett.*, **39**,
732 <https://doi.org/10.1029/2012GL054172>.

- 733 Gettelman, A., and Coauthors, 2019: High Climate Sensitivity in the Community Earth
734 System Model Version 2 (CESM2). *Geophys. Res. Lett.*, **46**, 8329–8337,
735 <https://doi.org/10.1029/2019GL083978>.
- 736 Golaz, J.-C., and Coauthors, 2019: The DOE E3SM Coupled Model Version 1: Overview
737 and Evaluation at Standard Resolution. *J. Adv. Model. Earth Syst.*, **11**, 2089–
738 2129, <https://doi.org/10.1029/2018MS001603>.
- 739 Green, J. K., A. G. Konings, S. H. Alemohammad, J. Berry, D. Entekhabi, J. Kolassa,
740 J.-E. Lee, and P. Gentine, 2017: Regionally strong feedbacks between the
741 atmosphere and terrestrial biosphere. *Nat. Geosci.*, **10**, 410–414,
742 <https://doi.org/10.1038/ngeo2957>.
- 743 Gregory, J. M., and P. M. Forster, 2008: Transient climate response estimated from
744 radiative forcing and observed temperature change. *J. Geophys. Res.*
745 *Atmospheres*, **113**, <https://doi.org/10.1029/2008JD010405>.
- 746 ———, and Coauthors, 2004: A new method for diagnosing radiative forcing and climate
747 sensitivity. *Geophys. Res. Lett.*, **31**, <https://doi.org/10.1029/2003GL018747>.
- 748 Hansen, J., and Coauthors, 2005: Efficacy of climate forcings. *J. Geophys. Res.*
749 *Atmospheres*, **110**, <https://doi.org/10.1029/2005JD005776>.
- 750 Hense, I., I. Stemmler, and S. Sonntag, 2017: Ideas and perspectives: climate-relevant
751 marine biologically driven mechanisms in Earth system models. *Biogeosciences*,
752 **14**, 403–413, <https://doi.org/10.5194/bg-14-403-2017>.
- 753 Hungate, B. A., M. Reichstein, P. Dijkstra, D. Johnson, G. Hymus, J. D. Tenhunen, C.
754 R. Hinkle, and B. G. Drake, 2002: Evapotranspiration and soil water content in a

755 scrub-oak woodland under carbon dioxide enrichment. *Glob. Change Biol.*, **8**,
756 289–298, <https://doi.org/10.1046/j.1365-2486.2002.00468.x>.

757 Jones, C. D., and Coauthors, 2016: C4MIP -- The Coupled Climate–Carbon Cycle
758 Model Intercomparison Project: experimental protocol for CMIP6. *Geosci. Model
759 Dev.*, **9**, 2853–2880, <https://doi.org/10.5194/gmd-9-2853-2016>.

760 Joshi, M. M., J. M. Gregory, M. J. Webb, D. M. H. Sexton, and T. C. Johns, 2008:
761 Mechanisms for the land/sea warming contrast exhibited by simulations of
762 climate change. *Clim. Dyn.*, **30**, 455–465, [https://doi.org/10.1007/s00382-007-](https://doi.org/10.1007/s00382-007-0306-1)
763 0306-1.

764 Kooperman, G. J., Y. Chen, F. M. Hoffman, C. D. Koven, K. Lindsay, M. S. Pritchard,
765 A. L. S. Swann, and J. T. Randerson, 2018: Forest response to rising CO₂ drives
766 zonally asymmetric rainfall change over tropical land. *Nat. Clim. Change*, **8**, 434–
767 440, <https://doi.org/10.1038/s41558-018-0144-7>.

768 Laguë, M. M., and A. L. S. Swann, 2016: Progressive Midlatitude Afforestation: Impacts
769 on Clouds, Global Energy Transport, and Precipitation. *J. Clim.*, **29**, 5561–5573,
770 <https://doi.org/10.1175/JCLI-D-15-0748.1>.

771 ———, G. B. Bonan, and A. L. S. Swann, 2019: Separating the Impact of Individual Land
772 Surface Properties on the Terrestrial Surface Energy Budget in both the Coupled
773 and Uncoupled Land–Atmosphere System. *J. Clim.*, **32**, 5725–5744,
774 <https://doi.org/10.1175/JCLI-D-18-0812.1>.

775 Langenbrunner, B., M. S. Pritchard, G. J. Kooperman, and J. T. Randerson, 2019: Why
776 Does Amazon Precipitation Decrease When Tropical Forests Respond to

- 777 Increasing CO₂? *Earths Future*, **7**, 450–468,
778 <https://doi.org/10.1029/2018EF001026>.
- 779 Leakey, A. D. B., E. A. Ainsworth, C. J. Bernacchi, A. Rogers, S. P. Long, and D. R.
780 Ort, 2009: Elevated CO₂ effects on plant carbon, nitrogen, and water relations:
781 six important lessons from FACE. *J. Exp. Bot.*, **60**, 2859–2876,
782 <https://doi.org/10.1093/jxb/erp096>.
- 783 Leeuwen, T. T. van, A. J. Frank, Y. Jin, P. Smyth, M. L. Goulden, G. R. van der Werf,
784 and J. T. Randerson, 2011: Optimal use of land surface temperature data to
785 detect changes in tropical forest cover. *J. Geophys. Res. Biogeosciences*, **116**,
786 <https://doi.org/10.1029/2010JG001488>.
- 787 Lemordant, L., and P. Gentine, 2019: Vegetation Response to Rising CO₂ Impacts
788 Extreme Temperatures. *Geophys. Res. Lett.*, **46**, 1383–1392,
789 <https://doi.org/10.1029/2018GL080238>.
- 790 —, —, M. Stéfanon, P. Drobinski, and S. Fatichi, 2016: Modification of land-
791 atmosphere interactions by CO₂ effects: Implications for summer dryness and
792 heat wave amplitude. *Geophys. Res. Lett.*, **43**, 10,240–10,248,
793 <https://doi.org/10.1002/2016GL069896>.
- 794 —, —, A. S. Swann, B. I. Cook, and J. Scheff, 2018: Critical impact of vegetation
795 physiology on the continental hydrologic cycle in response to increasing CO₂.
796 *Proc. Natl. Acad. Sci.*, **115**, 4093–4098, <https://doi.org/10.1073/pnas.1720712115>.
- 797 Levis, S., J. A. Foley, and D. Pollard, 2000: Large-Scale Vegetation Feedbacks on a
798 Doubled CO₂ Climate. *J. Clim.*, **13**, 1313–1325, [https://doi.org/10.1175/1520-0442\(2000\)013<1313:LSVFOA>2.0.CO;2](https://doi.org/10.1175/1520-0442(2000)013<1313:LSVFOA>2.0.CO;2).

800 Lian, X., and Coauthors, 2018: Partitioning global land evapotranspiration using CMIP5
801 models constrained by observations. *Nat. Clim. Change*, **8**, 640–646,
802 <https://doi.org/10.1038/s41558-018-0207-9>.

803 Lin, Y.-S., and Coauthors, 2015: Optimal stomatal behaviour around the world. *Nat.*
804 *Clim. Change*, **5**, 459–464, <https://doi.org/10.1038/nclimate2550>.

805 Lutsko, N. J., and M. Popp, 2019: Probing the Sources of Uncertainty in Transient
806 Warming on Different Timescales. *Geophys. Res. Lett.*, **46**, 11367–11377,
807 <https://doi.org/10.1029/2019GL084018>.

808 Marshall, J., J. R. Scott, K. C. Armour, J.-M. Campin, M. Kelley, and A. Romanou,
809 2015: The ocean’s role in the transient response of climate to abrupt greenhouse
810 gas forcing. *Clim. Dyn.*, **44**, 2287–2299, [https://doi.org/10.1007/s00382-014-2308-](https://doi.org/10.1007/s00382-014-2308-0)
811 [0](https://doi.org/10.1007/s00382-014-2308-0).

812 Medlyn, B. E., and Coauthors, 2011: Reconciling the optimal and empirical approaches
813 to modelling stomatal conductance. *Glob. Change Biol.*, **17**, 2134–2144,
814 <https://doi.org/10.1111/j.1365-2486.2010.02375.x>.

815 Norby, R. J., and D. R. Zak, 2011: Ecological Lessons from Free-Air CO₂ Enrichment
816 (FACE) Experiments. *Annu. Rev. Ecol. Evol. Syst.*, **42**, 181–203,
817 <https://doi.org/10.1146/annurev-ecolsys-102209-144647>.

818 O’ishi, R., A. Abe-Ouchi, I. C. Prentice, and S. Sitch, 2009: Vegetation dynamics and
819 plant CO₂ responses as positive feedbacks in a greenhouse world. *Geophys. Res.*
820 *Lett.*, **36**, <https://doi.org/10.1029/2009GL038217>.

821 Parsons, L. A., K. Brennan, R. Jnglin Wills, and C. Proistosescu, In Revision:
822 Magnitudes and spatial patterns of interdecadal temperature variability in
823 CMIP6. *Geophys. Res. Lett.*,

824 Piao, S., and Coauthors, 2013: Evaluation of terrestrial carbon cycle models for their
825 response to climate variability and to CO₂ trends. *Glob. Change Biol.*, **19**, 2117–
826 2132, <https://doi.org/10.1111/gcb.12187>.

827 Pu, B., and R. E. Dickinson, 2012: Examining vegetation feedbacks on global warming
828 in the Community Earth System Model. *J. Geophys. Res. Atmospheres*, **117**,
829 <https://doi.org/10.1029/2012JD017623>.

830 Roe, G., 2009: Feedbacks, Timescales, and Seeing Red. *Annu. Rev. Earth Planet. Sci.*,
831 **37**, 93–115, <https://doi.org/10.1146/annurev.earth.061008.134734>.

832 Schimel, D., B. B. Stephens, and J. B. Fisher, 2015: Effect of increasing CO₂ on the
833 terrestrial carbon cycle. *Proc. Natl. Acad. Sci.*, **112**, 436–441,
834 <https://doi.org/10.1073/pnas.1407302112>.

835 Sellers, P. J., and Coauthors, 1996: Comparison of Radiative and Physiological Effects
836 of Doubled Atmospheric CO₂ on Climate. *Science*, **271**, 1402–1406,
837 <https://doi.org/10.1126/science.271.5254.1402>.

838 Sherwood, S. C., S. Bony, O. Boucher, C. Bretherton, P. M. Forster, J. M. Gregory, and
839 B. Stevens, 2015: Adjustments in the Forcing-Feedback Framework for
840 Understanding Climate Change. *Bull. Am. Meteorol. Soc.*, **96**, 217–228,
841 <https://doi.org/10.1175/BAMS-D-13-00167.1>.

842 Skinner, C. B., C. J. Poulsen, and J. S. Mankin, 2018: Amplification of heat extremes by
843 plant CO₂ physiological forcing. *Nat. Commun.*, **9**, 1–11,
844 <https://doi.org/10.1038/s41467-018-03472-w>.

845 Smith, W. K., S. C. Reed, C. C. Cleveland, A. P. Ballantyne, W. R. L. Anderegg, W. R.
846 Wieder, Y. Y. Liu, and S. W. Running, 2016: Large divergence of satellite and
847 Earth system model estimates of global terrestrial CO₂ fertilization. *Nat. Clim.*
848 *Change*, **6**, 306–310, <https://doi.org/10.1038/nclimate2879>.

849 Swann, A. L. S., I. Y. Fung, and J. C. H. Chiang, 2012: Mid-latitude afforestation shifts
850 general circulation and tropical precipitation. *Proc. Natl. Acad. Sci.*, **109**, 712–
851 716, <https://doi.org/10.1073/pnas.1116706108>.

852 ———, ———, Y. Liu, and J. C. H. Chiang, 2014: Remote Vegetation Feedbacks and the
853 Mid-Holocene Green Sahara. *J. Clim.*, **27**, 4857–4870,
854 <https://doi.org/10.1175/JCLI-D-13-00690.1>.

855 ———, F. M. Hoffman, C. D. Koven, and J. T. Randerson, 2016: Plant responses to
856 increasing CO₂ reduce estimates of climate impacts on drought severity. *Proc.*
857 *Natl. Acad. Sci.*, **113**, 10019–10024, <https://doi.org/10.1073/pnas.1604581113>.

858 Tang, T., and Coauthors, 2019: Comparison of Effective Radiative Forcing Calculations
859 Using Multiple Methods, Drivers, and Models. *J. Geophys. Res. Atmospheres*,
860 **124**, 4382–4394, <https://doi.org/10.1029/2018JD030188>.

861 Vargas Zeppetello, L. R., A. Donohoe, and D. S. Battisti, 2019: Does Surface
862 Temperature Respond to or Determine Downwelling Longwave Radiation?
863 *Geophys. Res. Lett.*, **46**, 2781–2789, <https://doi.org/10.1029/2019GL082220>.

864 Vial, J., J.-L. Dufresne, and S. Bony, 2013: On the interpretation of inter-model spread
865 in CMIP5 climate sensitivity estimates. *Clim. Dyn.*, **41**, 3339–3362,
866 <https://doi.org/10.1007/s00382-013-1725-9>.

867 Vico, G., S. Manzoni, S. Palmroth, and G. Katul, 2011: Effects of stomatal delays on
868 the economics of leaf gas exchange under intermittent light regimes. *New Phytol.*,
869 **192**, 640–652, <https://doi.org/10.1111/j.1469-8137.2011.03847.x>.

870 Webb, M. J., and Coauthors, 2017: The Cloud Feedback Model Intercomparison Project
871 (CFMIP) contribution to CMIP6. *Geosci. Model Dev.*, **10**, 359–384,
872 <https://doi.org/10.5194/gmd-10-359-2017>.

873 Wolz, K. J., T. M. Wertin, M. Abordo, D. Wang, and A. D. B. Leakey, 2017: Diversity
874 in stomatal function is integral to modelling plant carbon and water fluxes. *Nat.*
875 *Ecol. Evol.*, **1**, 1292–1298, <https://doi.org/10.1038/s41559-017-0238-z>.

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877

878 **8. Tables**

879

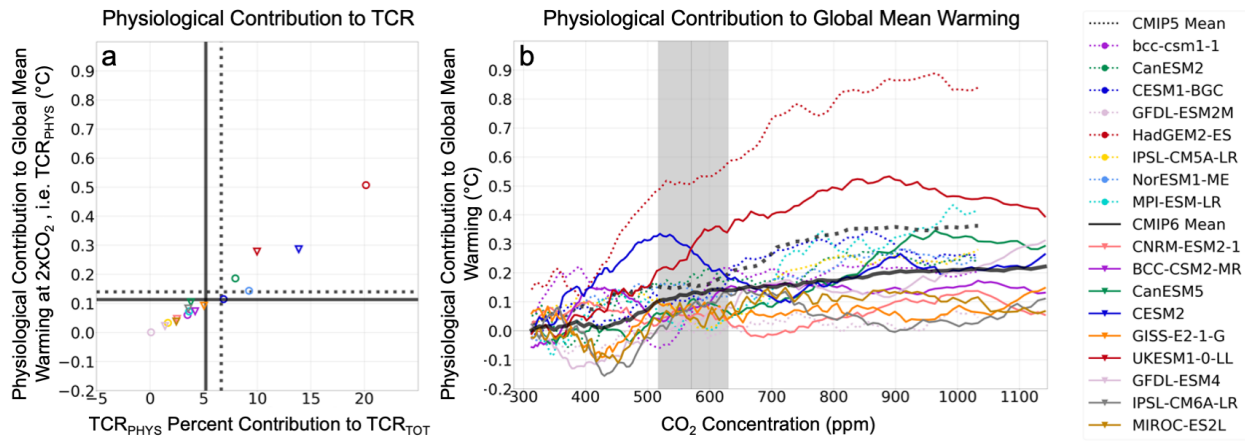
Experiment	CMIP5 Experiment Name	CMIP6 Experiment Name	Influence of CO ₂ Concentration on:		
			Land	Ocean	Atmosphere
FULL	1pctCO2	1pctCO2	1% per year	1% per year	1% per year
PHYS	esmFixClim1	1pctCO2-bgc	1% per year	1% per year	Pre-industrial
RAD	exmFdbk1	1pctCO2-rad	Pre-industrial	Pre-industrial	1% per year
PI	piControl	piControl	Pre-industrial	Pre-industrial	Pre-industrial

880 **TABLE 1.** Summary of CMIP experiments used.

Modeling Center	CMIP5 Model TCR								CMIP6 Model TCR											
	Model Name	FULL			RAD		PHYS-PI		TOT-RAD		Model Name	FULL			RAD		PHYS-PI		TOT-RAD	
		°C	°C	%	°C	%	°C	%	°C	%		°C	°C	%	°C	%	°C	%		
Beijing Climate Center (BCC)	bcc-csm1-1	1.73	1.67	96.5%	0.05	2.8%	0.06	3.5%	BCC-CSM2-MR	1.73	1.66	95.8%	0.54	31.4%	0.07	4.2%				
Canadian Centre for Climate Modelling and Analysis (CCCma)	CanESM2	2.34	2.16	92.0%	0.15	6.5%	0.18	8.0%	CanESM5	2.74	2.64	96.2%	0.04	1.5%	0.10	3.8%				
National Center for Atmospheric Research (NCAR)	CESM1-BGC	1.68	1.56	93.2%	0.11	6.6%	0.12	6.8%	CESM2	2.06	1.78	86.1%	0.11	5.2%	0.29	13.9%				
NOAA Geophysical Fluid Dynamics Laboratory (NOAA-GFDL)	GFDL-ESM2M	1.35	1.35	99.9%	0.05	3.4%	0.00	0.1%	GFDL-ESM4	1.61	1.58	98.6%	0.17	10.7%	0.02	1.4%				
Met Office Hadley Centre (MOHC)	HadGEM2-ES	2.52	2.01	79.9%	0.37	14.6%	0.51	20.1%	UKESM1-0-LL	2.79	2.51	90.0%	0.17	6.0%	0.28	10.0%				
Institut Pierre Simon Laplace (IPSL)	IPSL-CM5A-LR	2.00	1.97	98.3%	0.11	5.6%	0.03	1.7%	IPSL-CM6A-LR	2.31	2.23	96.4%	0.17	7.3%	0.08	3.6%				
Norwegian Climate Centre (NCC)	NorESM1-ME	1.56	1.42	90.8%	0.08	5.3%	0.14	9.2%	-	-	-	-	-	-	-	-				
Max Planck Institute for Meteorology (MPI-M)	MPI-ESM-LR	2.02	1.95	96.4%	0.20	9.9%	0.07	3.6%	-	-	-	-	-	-	-	-				
Centre National de Recherches Météorologiques (CNRM-CERFACS)	-	-	-	-	-	-	-	-	CNRM-ESM2-1	1.84	1.80	97.5%	-0.15	-8.0%	0.05	2.5%				
NASA Goddard Institute for Space Studies (NASA-GISS)	-	-	-	-	-	-	-	-	GISS-E2-1-G	1.82	1.73	95.0%	0.10	5.7%	0.09	5.0%				
Japan Agency for Marine-Earth Science and Technology (JAMSTEC)	-	-	-	-	-	-	-	-	MIROC-ES2L	1.55	1.52	97.6%	0.07	4.8%	0.04	2.4%				
Mean	All Models	1.90	1.76	93.4%	0.10	6.8%	0.14	6.6%	All Models	2.05	1.94	94.8%	0.14	7.2%	0.11	5.2%				
	<i>Consistent Model Subset</i>	<i>1.94</i>	<i>1.79</i>	<i>93.3%</i>	<i>0.14</i>	<i>6.6%</i>	<i>0.15</i>	<i>6.7%</i>	<i>Consistent Model Subset</i>	<i>2.21</i>	<i>2.06</i>	<i>93.9%</i>	<i>0.20</i>	<i>10.4%</i>	<i>0.14</i>	<i>6.1%</i>				
Standard Deviation	All Models	0.40	0.30	6.3%	0.11	3.8%	0.16	6.3%	All Models	0.46	0.41	4.1%	0.18	10.5%	0.10	4.1%				
	<i>Consistent Model Subset</i>	<i>0.44</i>	<i>0.31</i>	<i>7.2%</i>	<i>0.12</i>	<i>4.2%</i>	<i>0.19</i>	<i>7.2%</i>	<i>Consistent Model Subset</i>	<i>0.50</i>	<i>0.45</i>	<i>4.8%</i>	<i>0.18</i>	<i>10.7%</i>	<i>0.11</i>	<i>4.8%</i>				

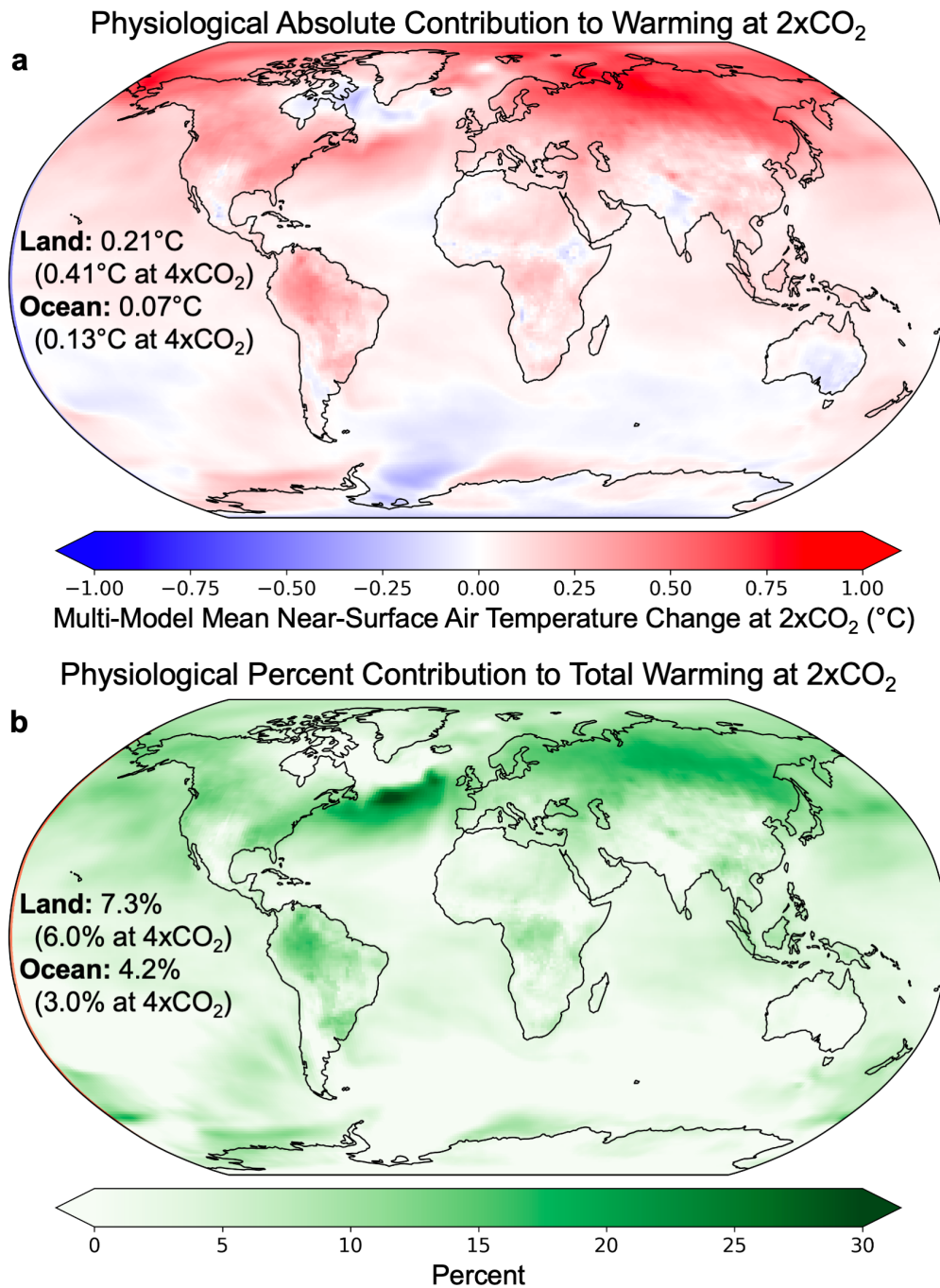
882 **TABLE 2.** TCR_{FULL} , TCR_{RAD} , and TCR_{PHYS} by model, where TCR_{PHYS} is calculated by both PHYS-PI and TOT-RAD.
883 The consistent model subset refers to the six models for which the necessary model output is available for both CMIP5 and
884 CMIP6. For the summary statistics in the last four rows, the percentages refer to the mean and standard deviations of the
885 percent contributions across models.

886 **9. Figures**



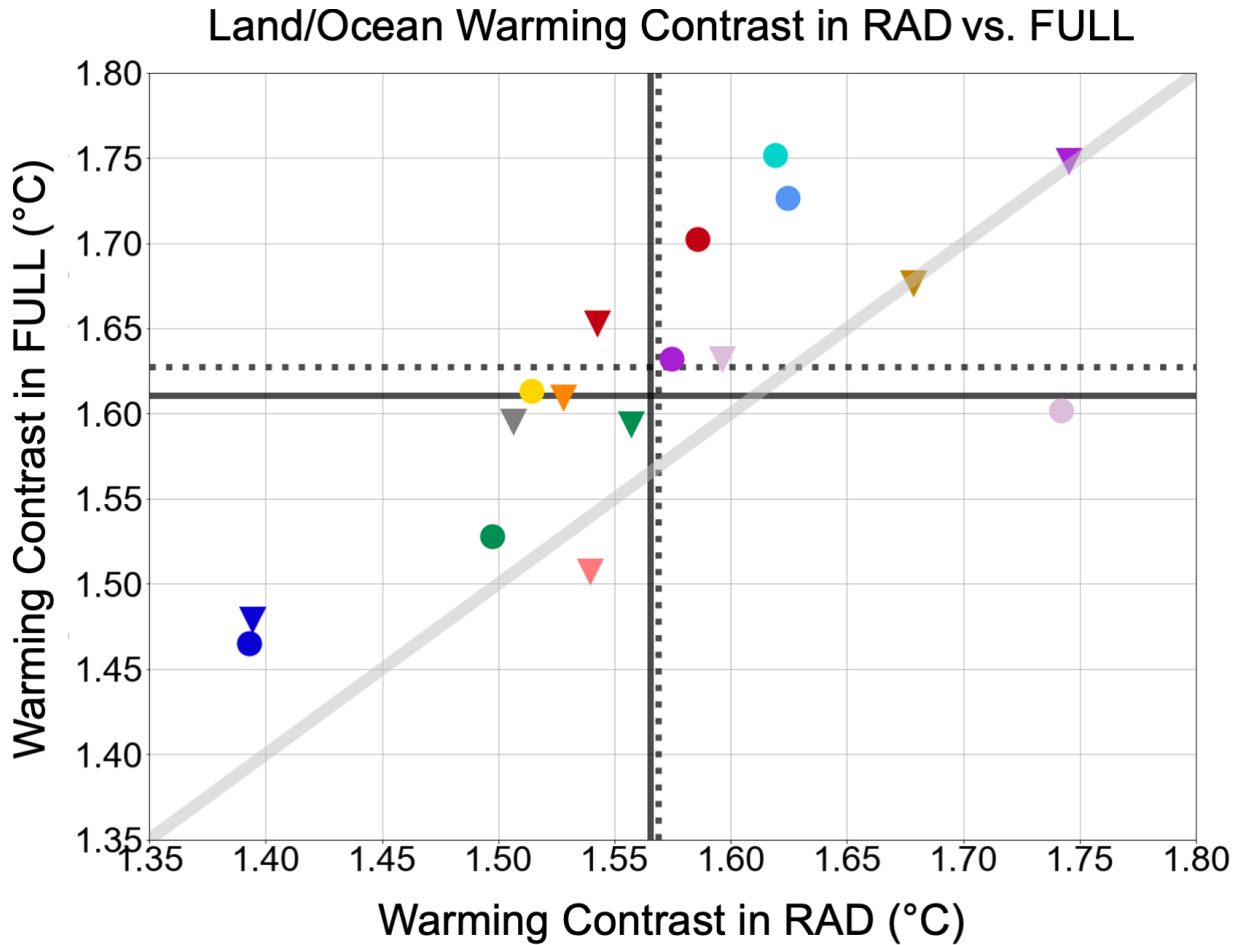
887

888 **FIGURE 1.** Physiological contribution to global mean warming. (a) The relationship
 889 between the relative contribution of TCR_{PHYS} to the full TCR (i.e. TCR_{PHYS}/TCR_{FULL})
 890 and the absolute magnitude of TCR_{PHYS}, as calculated by FULL-RAD. Marker types
 891 indicate CMIP phase (CMIP5: circles; CMIP6: triangles) and colors indicate modeling
 892 center. Lines demarcate the multi-model mean for CMIP5 (dashed) and CMIP6 (solid).
 893 Note that the set of models included in the average differs between CMIP5 and CMIP6.
 894 (b) Global mean physiologically-driven temperature change as a function of CO₂
 895 concentration, calculated from FULL-RAD and smoothed with a 20-year boxcar. The
 896 dark gray vertical line marks the time of CO₂ doubling, and the light gray bar indicates
 897 the 20-year period surrounding the time of CO₂ doubling. Colors indicate modeling
 898 center as in (a), and line types indicate CMIP phase (CMIP5: dashed; CMIP6: solid).



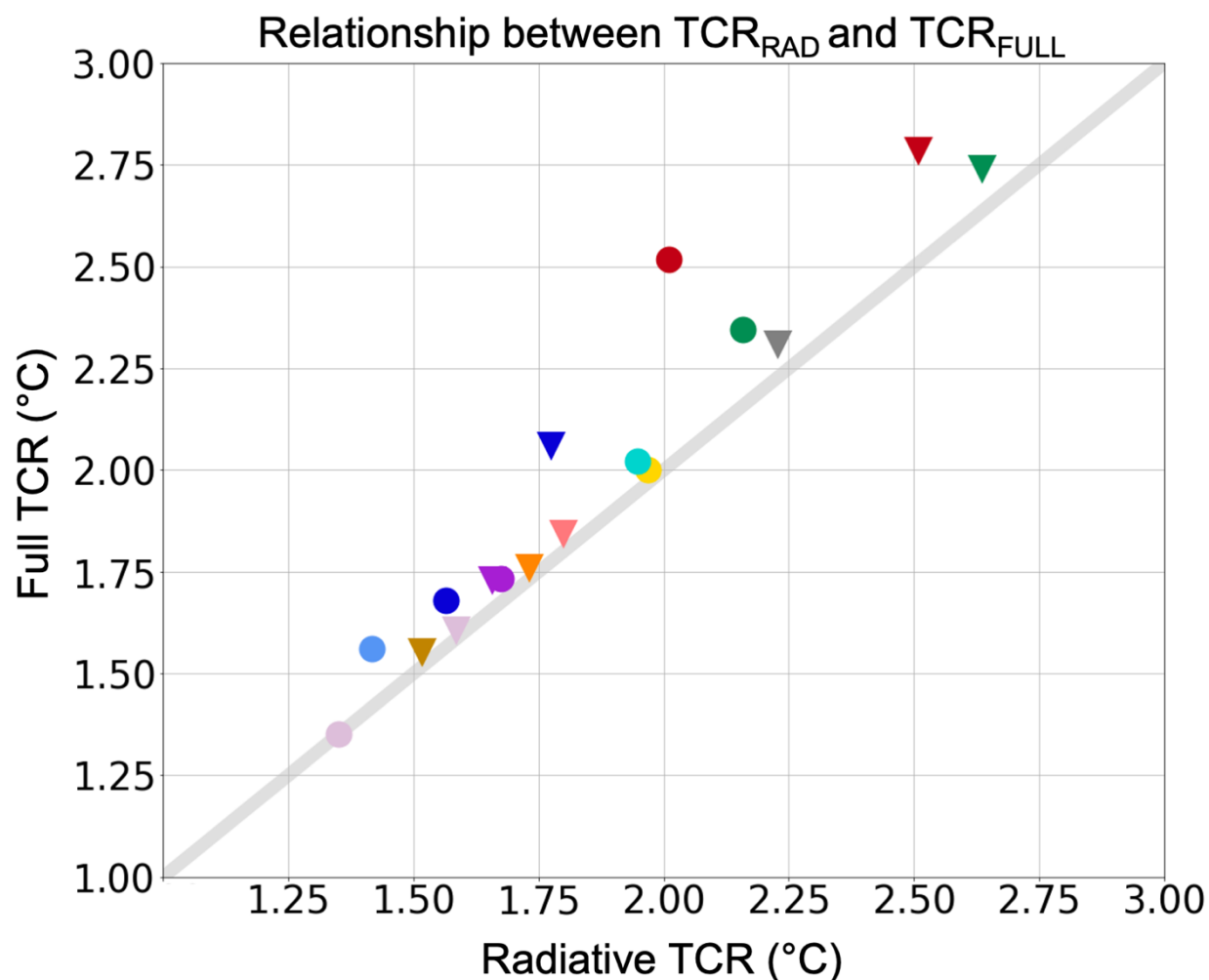
899

900 **FIGURE 2.** Spatial pattern of (a) absolute physiologically-driven warming and (b)
 901 physiological percent contribution to total warming at 2xCO₂, where physiologically-
 902 driven warming is calculated by FULL-RAD. Multi-model means include the 9 CMIP6
 903 models.

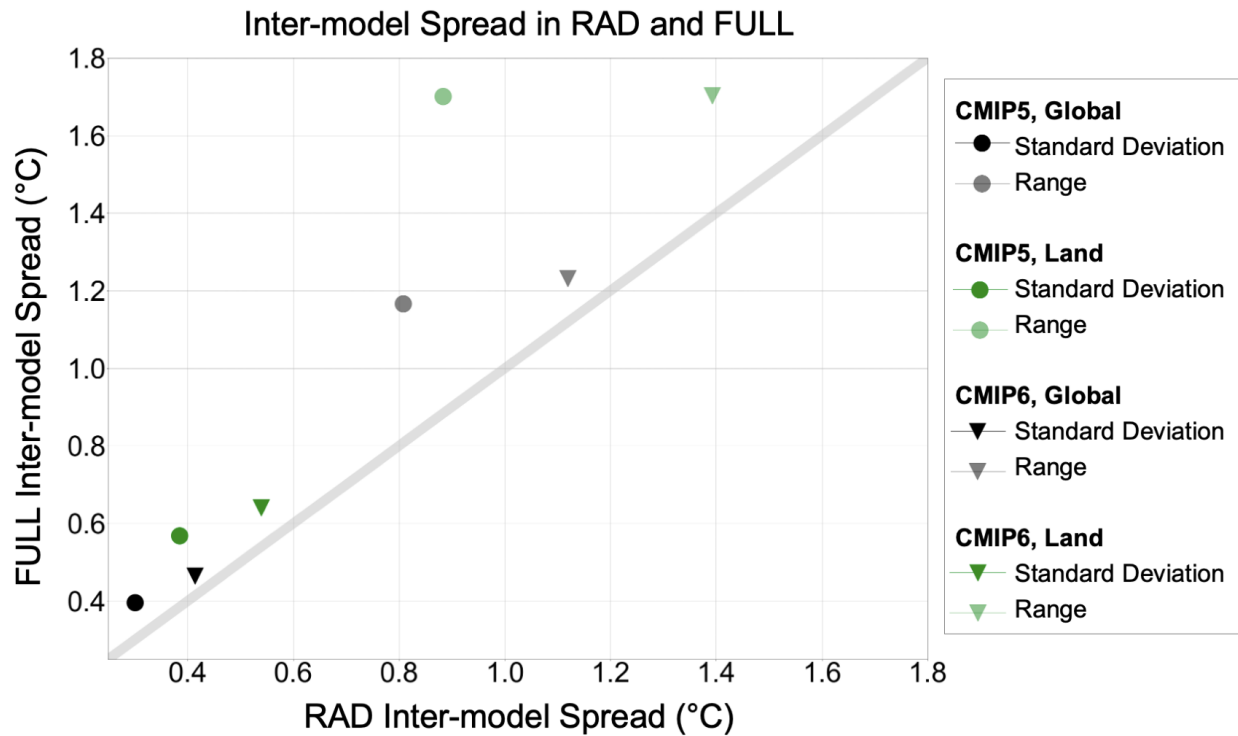


904

905 **FIGURE 3.** The relationship between the land/ocean warming contrast (the ratio of
 906 the change in non-glaciated land temperature to the change in ocean temperature) from
 907 RAD (RAD-PI) and FULL (FULL-PI). The gray 1:1 line is where we would expect all
 908 models to be if the warming contrast were entirely caused by the radiative effects of
 909 CO₂. Physiology's addition to the warming contrast is the vertical distance between the
 910 gray 1:1 line and each point. Marker types indicate CMIP phase (CMIP5: circles;
 911 CMIP6: triangles) and colors indicate modeling center as in Figure 1. Lines demarcate
 912 the multi-model average for CMIP5 (dashed) and CMIP6 (solid). Note that the set of
 913 models included in the average differs between CMIP5 and CMIP6.



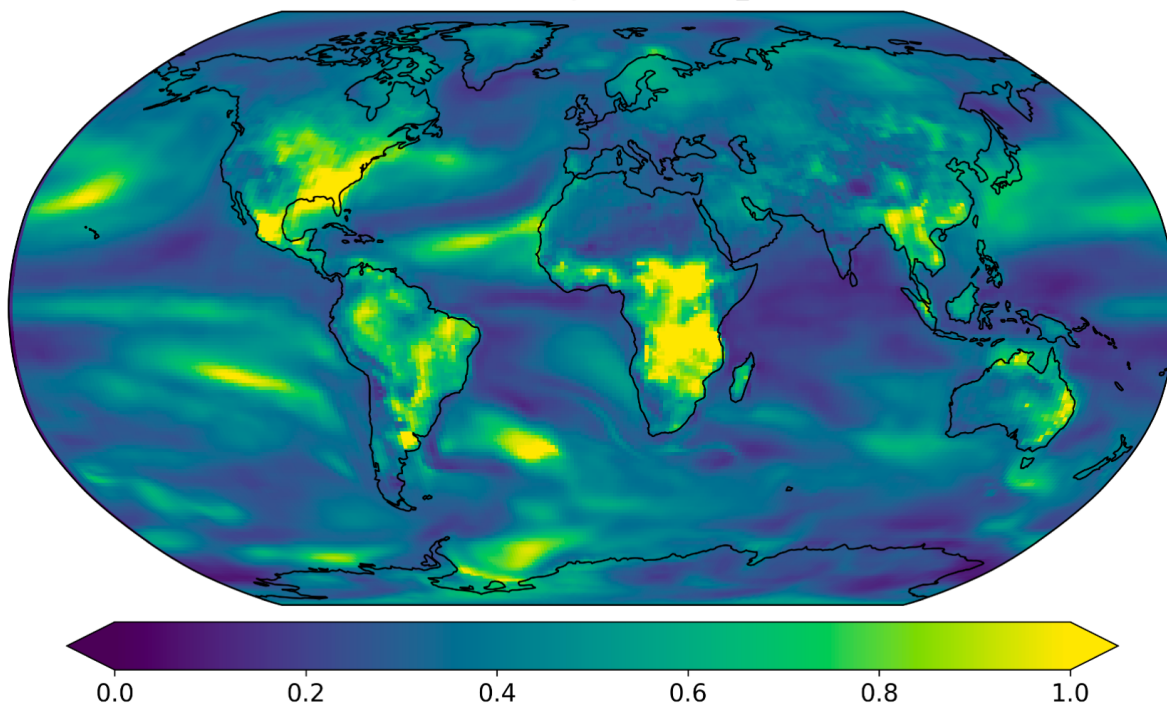
914
 915 **FIGURE 4.** The relationship between TCR_{RAD} (RAD-PI) and TCR_{FULL} (FULL-PI).
 916 The gray 1:1 line is where we would expect all models to be if the TCR were entirely
 917 caused by the radiative effects of CO_2 . The added warming from the physiological effect
 918 is the vertical distance between the gray 1:1 line and each point. Marker types indicate
 919 CMIP phase (CMIP5: circles; CMIP6: triangles) and colors indicate modeling center as
 920 in Figure 1.



922

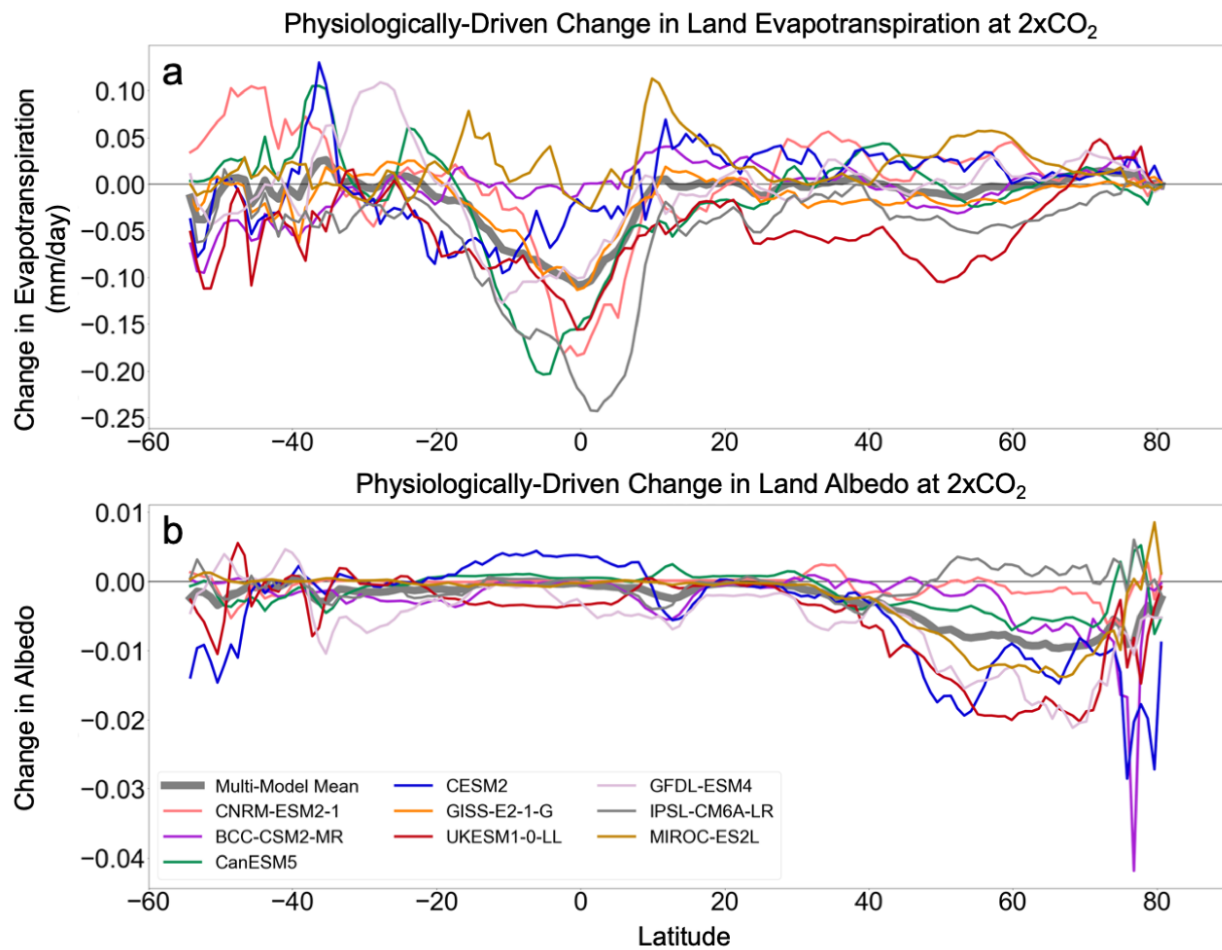
923 **FIGURE 5.** Physiology's contribution to inter-model spread in global mean warming.
 924 Inter-model spread in global (black and grey) and land only (green) warming in FULL
 925 (FULL-PI) and RAD (RAD-PI), as quantified by the full inter-model range and the
 926 standard deviation. The 1:1 line is where we would expect all models to be if inter-model
 927 spread in warming were entirely caused by the radiative effects of CO₂. The added inter-
 928 model spread from the physiological effect is the vertical distance between the gray 1:1
 929 line and each point. Marker types indicate CMIP phase (CMIP5: circles; CMIP6:
 930 triangles).

Physiology's Relative Contribution to Uncertainty in Total Warming at 2xCO₂



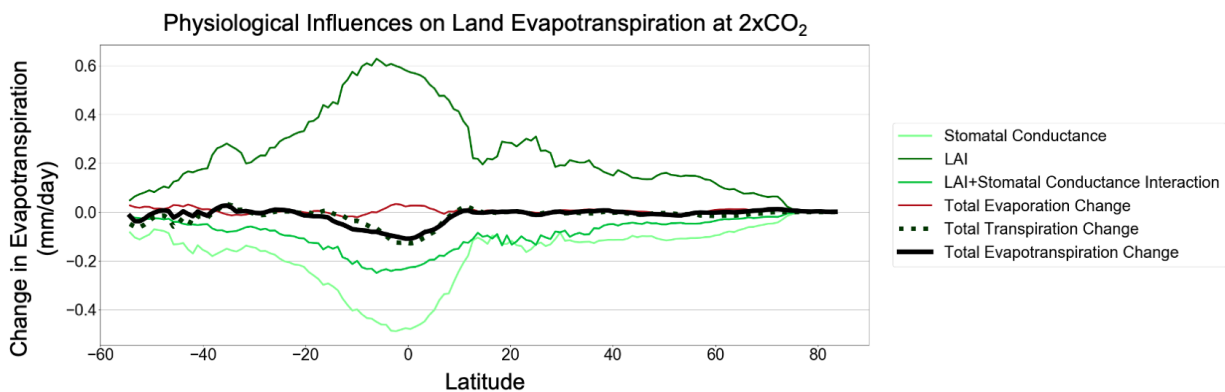
Ratio of the standard deviation of TCR_{PHYS} to the standard deviation of TCR_{RAD}

931
932 **FIGURE 6.** Spatial pattern of physiology's relative contribution to inter-model spread
933 in CO₂-forced warming. The ratio of the standard deviation (SD; at each grid cell,
934 across models) of physiologically forced warming (calculated from FULL-RAD) to the
935 SD of radiatively forced warming (calculated from RAD-PI) at 2xCO₂ for CMIP6
936 models. A value of 1 means that the physiological and radiative effects of CO₂
937 contribute equally to the total uncertainty in local warming at 2xCO₂ across models.



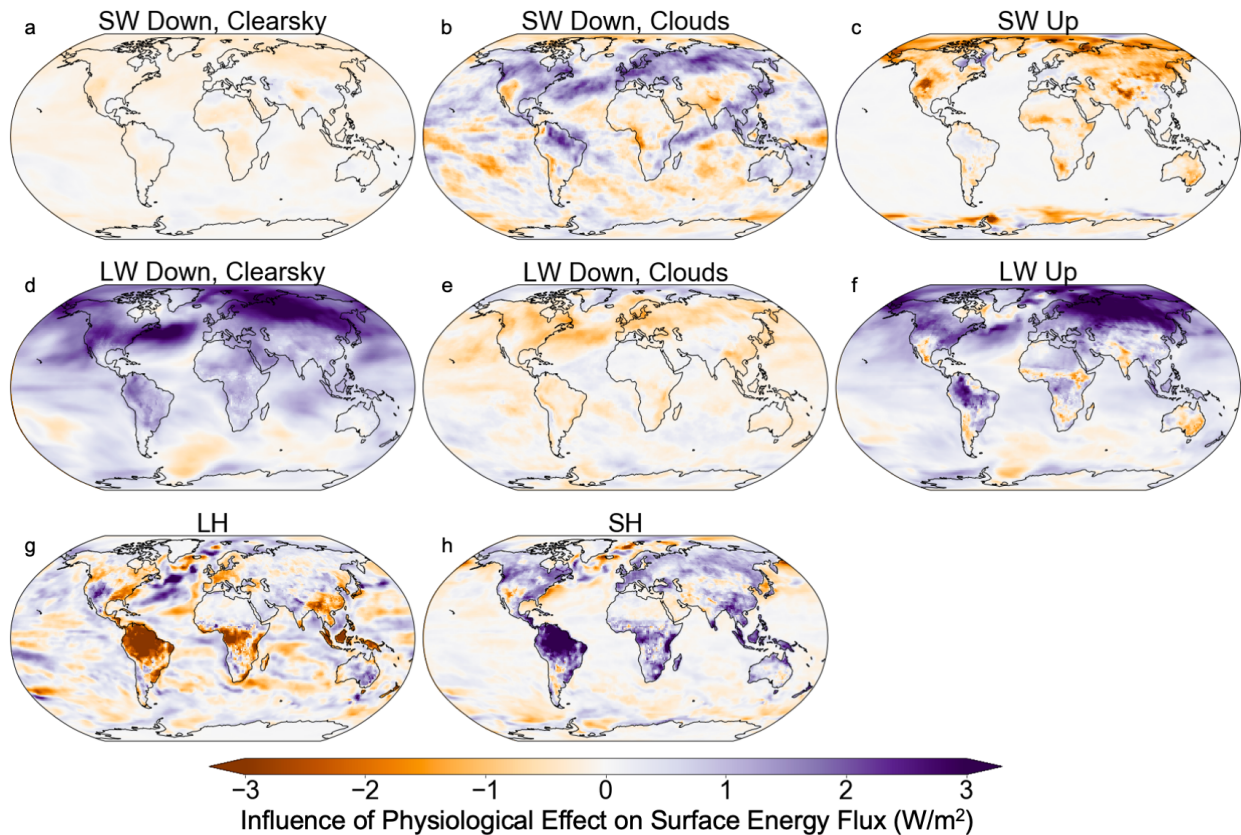
939

940 **FIGURE 7.** Land zonal means of physiologically-driven changes in (a)
 941 evapotranspiration and (b) albedo at 2xCO₂ for CMIP6 models, as calculated by FULL-
 942 RAD.



943

944 **FIGURE 8.** Zonal means of how much physiologically-driven changes in different land
 945 processes (stomatal conductance, LAI, and evaporation) contribute to the total multi-
 946 model mean physiologically-driven change in land evapotranspiration. Multi-model
 947 means in this figure are averaged across all CMIP6 models for which model output is
 948 available, which consists of up to 9 models. Transpiration and LAI data necessary for
 949 this partitioning were not available for GFDL-ESM4, so this model is only included in
 950 the multi-model mean for the total evapotranspiration change. The total
 951 evapotranspiration change (black line) is the same as the multi-model mean change in
 952 evapotranspiration shown in Figure 7a.



954

955

956 **FIGURE 9.** Spatial pattern of multi-model mean physiologically-driven changes in
 957 surface energy fluxes as calculated by FULL-RAD at the point of CO₂ doubling
 958 (averaged over years 61-80) for (a) clear-sky downwelling shortwave radiation, (b)
 959 cloudy downwelling shortwave radiation, (c) upwelling shortwave radiation, (d) clear-
 960 sky downwelling longwave radiation, (e) cloudy downwelling longwave radiation, (f)
 961 upwelling longwave radiation, (g) latent heat, and (h) sensible heat. Multi-model means
 962 include all CMIP6 models for which model output is available; this consists of up to 9
 963 models. Data for some surface energy fluxes were not available for the following models:
 964 GFDL-ESM4 (panels a, b, d, and e), GISS-E2-1-G, 3 (panels c and h) and CNRM-
 965 ESM2-1 (panels d and e).